AUSTRALIAN ARTHRODIRES

BY

ERROL WHITE

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CONTENTS

SYNOPSIS

A small collection of arthrodire remains is described from the Middle Devonian strata in the Burrinjuck Dam area, New South Wales. Three, possibly four genera are represented, two of them new, and a third, congeneric with Hills's '*Coccosteus osseus*', shows part of the neurocranium: this form is considered to be a brachythoracid. A note is added on *Notopetalichthys*, from the same beds. The bearing of this new evidence on existing theories on the development of arthrodire fins and armour and on the classification of the group is discussed and tentative new hypotheses are put forward.

I. INTRODUCTION

IN 1939, just before the war, Mr. R. Bedford, Director of the Kyancutta Museum, South Australia, sent to the British Museum for identification five specimens showing the remains of fishes that Mr. W. E. Williams, of Cootamundra, New South Wales, had collected from the Middle Devonian marine limestones of the Burrinjuck Dam area, New South Wales, some 35 miles north-west of the federal capital, Canberra.

Owing to the war and subsequent dislocation caused by the evacuation of part of the collections and damage to the Museum, it was not until ten years later that I was able to take up the study of the specimens seriously. Although for the most part

fragmentary, they were extraordinarily well preserved and bid fair to show structures rarely seen in these animals. The external features had been freed from the dark grey limestone matrix with much patient skill by Mr. Bedford, but it was decided to employ the acetic acid process (Toombs, 1948) in an effort to expose some of the delicate inner structures that appeared to be present in section on the fractured surfaces. Owing to the cracked state as well as the natural delicacy of the bones the process proved to be a very long and tedious one, for only a small portion could be exposed to the acid at a time, and had then to be covered with a protective coat of cellulose while a neighbouring area was treated. Altogether the work, done at intervals, took well over a year, but was most skilfully carried out by Mr. H. A. Toombs.

The specimens eventually proved to be even more interesting and important than was at first supposed, and their discovery reflects great credit on their collector, Mr. W. E. Williams, with whom Mr. Bedford kindly put me in touch. Mr. Williams has now most generously presented them to the British Museum (Natural History) and has given me full information concerning the localities. The specimens are preserved in dark grey limestones from the Murrumbidgee Series, of Couvinian (lower Middle Devonian) age (Hills, 1941: 46), from two localities: (1) Taemas, on the Murrumbidgee River, where Süssmilch found the head of *Dipnorhynchus* [*Ganorhynchus*] *süssmilchi* (Eth.); and (2) Barber's, about 10 miles to the west-south-west on the Goodradigbee River.

The five specimens are all of arthrodires, representing at least four genera, of which two are doubtless new. They comprise:

1. The greater part of the body-armour of a new arctolepid from Barber's.
2. An isolated brachythoracid gnathal plate from Barber's.
3. A slice of the head of a species related to the Victorian '*Coccosteus osseus*', from Taemas.
4. A fragment of a median dorsal plate, apparently of the same form as (3), from Taemas.
5. The complete paranuchal plate of a large new brachythoracid, from Taemas.

These then represent three, possibly four, diverse genera of arthrodires, and if we add the *Dipnorhynchus* and the petalichthyid, *Notopetalichthys*, from 'Goodra Vale' (Woodward, 1941—further note below), we have a total of five or six genera of fishes from seven specimens, and it is obvious that in the Burrinjuck area there is to be found a fish-fauna of outstanding importance among those in Devonian strata.

II. SYSTEMATIC DESCRIPTION

Order *ARCTOLEPIFORMES* (see p. 298)

Sub-order ARCTOLEPIDI

The most characteristic features of the arctolepid body-armour are the full development of the plates to cover all but the caudal region (with, I believe, the formation of a restricted pectoral fenestra) and hitherto the development of large pectoral spines. In the genus next described this last feature is absent, but there can be no
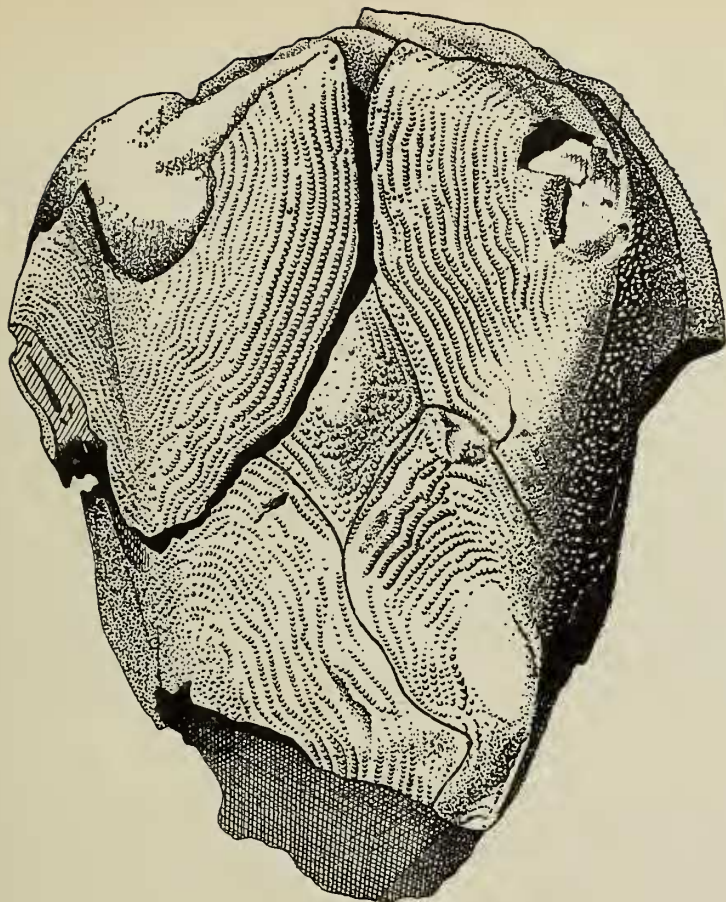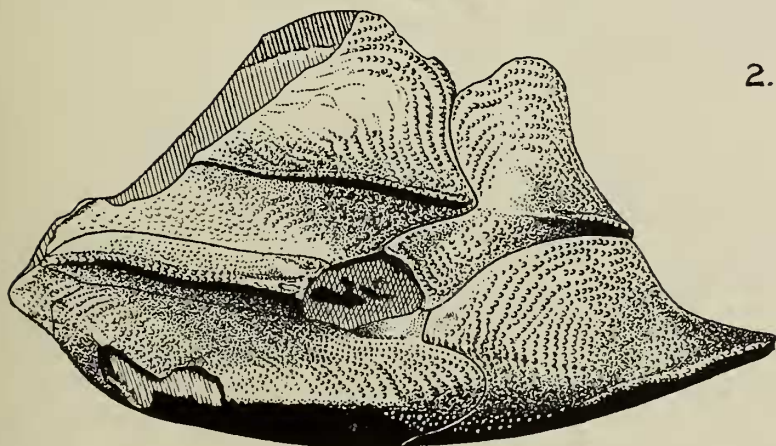
Williamsaspis bedfordi gen. et sp. nov.

Text-fig. 1. Body-armour, in ventral view. The holotype, P.27073, $\times 1\frac{1}{2}$.

Text-fig. 2. The same specimen, left side with right AVL removed, $\times 1\frac{1}{2}$.

doubt it must be included in this order, for the body-armour is otherwise quite typical.

It is also evident that the compass of the sub-order will have to be enlarged to include the more obvious derivative groups, such as the acanthothoracans which, unlike the ptyctodonts and phyllolepids, are not sufficiently specialized to warrant being considered as independent sub-orders.

Super-family WILLIAMSOSTEI

DIAGNOSIS. Arctolepids with the principal characters of the only family, the Williamsaspidae.

Family WILLIAMSASPIDAE

DIAGNOSIS. Arctolepids with rounded undersurface and spinal plate placed accordingly high on side without development of lateral spine. Lateral plates tall, the anterior with a broad mesial flange or apron at right angles to its lateral surface; the posterior, elbow-shaped with the lower anterior shank forming posterior dorsal margin of pectoral fenestra. Scapulo-coracoid cartilage completely invested with perichondrial bone, without scapular or lateral processes, reaching from posterior margin of pectoral fenestra to near midline in front, the coracoid processes being separated apparently by the thickness of the mesial surfaces of the interlateral plates.

Only one genus known.

Genus *WILLIAMSASPIS* nov.

DIAGNOSIS. As for family (only genus).

The genus is named in honour of Mr. W. E. Williams of Cootamundra, N.S.W., who collected this and the other new specimens described and generously presented them to the British Museum; the species in honour of Mr. R. Bedford of the Kyancutta Museum, S. Australia, who first developed the specimen and through whose interest the specimens came to the British Museum.

SPECIES. The genotype only.

Williamsaspis bedfordi sp. nov.
(PLS. 26–29; TEXT-FIGS. 1–18, 38, 39E)

DIAGNOSIS. As for family and genus (only species).

MATERIAL. The unique holotype, comprising the lower two-thirds of the body-armour (P.27073).

FORMATION AND LOCALITY. Middle Devonian; Barber's, Goodradigbee River, N.S.W.

DESCRIPTION OF SPECIMEN. This remarkable specimen (Pls. 26, 27; Text-figs. 1, 2) consists of the body-armour less the dorsal and dorsolateral plates. The anterior and posterior lateral, spinal, interlateral, anterior and posterior ventral plates of the left side, the anterior and posterior median ventral plates, and the imperfect posterior lateral and ventrolateral plates of the right side are all firmly in position; but the plates of the right fore-quarter, comprising the anterior lateral and ventrolateral
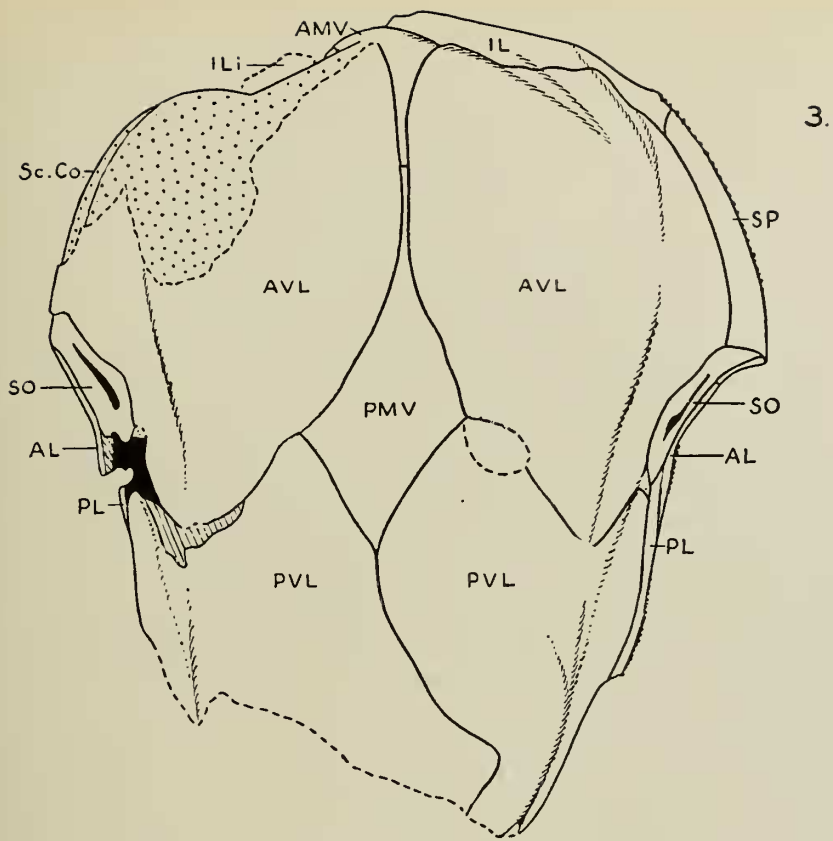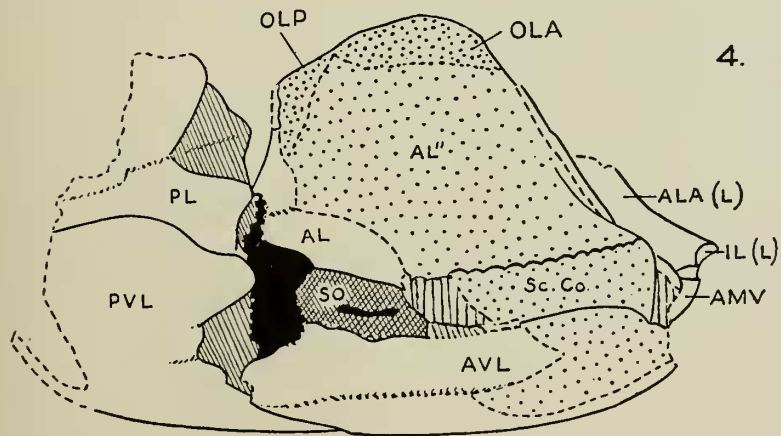
Williamsaspis bedfordi gen. et sp. nov.

TEXT-FIG. 3. Outline of body-armour in ventral view. The holotype, P.27073, $\times 1\frac{1}{2}$.

TEXT-FIG. 4. The same specimen, right side, slightly uptilted, $\times 1\frac{1}{2}$ approx.

(For explanation of lettering see pp. 303–304.)

plates, the interlateral and spinal with the fin-socket, have slipped as one piece a little downwards, forwards, and inwards, leaving a small gap between the side plates and forcing the right anterior ventrolaterals over the median plates.

The median bones and those of the left side are almost complete except for the central parts of the anterior lateral and ventrolateral and the tip of the posterior ventrolateral. Of the right plates (Text-figs. 4, 6) the whole of the spinal and all but a fragment of the interlaterals have been lost, leaving the impression of the mesial face of the scapulo-coracoid cartilage and fragments of perichondrial bone; while practically the whole of the anterior lateral is now preserved as an internal impression, and the front of the anterior ventrolateral, the hinder margin of the posterior lateral, and nearly half the posterior ventrolateral are missing. Nevertheless these are mechanical defects, the actual preservation of the bones being extremely fine. The specimen was very well developed by Mr. R. Bedford, to whom Mr. Williams, the discoverer, sent it, and was finished off in the British Museum (Natural History) by Mr. H. A. Toombs with the acetic acid treatment. The very finest details are now to be seen, some of the smaller plates being largely free of the matrix on the inside as well as the outside. It will be convenient to describe the specimen upside down, beginning with the ventral surface, which is virtually complete.

The length as preserved (and there are only a few millimetres missing from the posterior ventrolateral plates) is 7·2 cm., the maximum breadth, based on double the complete left side at the level of the tip of the spinal plate, is approximately 6·5 cm.

The median ventral plates (Pl. 26, fig. 1; Pl. 28, fig. 3; Text-figs. 3, 10) are large and in contact with one another, like those in *Coccosteus* (Heintz, 1938a: text-figs. 1, 7) and certain arctolepids such as *Euryaspis*, the anterior (AMV) being shaped like an axe-head with a rounded anterior margin fitted behind the interlateral plates at their junction, while the posterior plate (PMV) is diamond-shaped with the prolonged front angle truncated. Both plates are gently convex and the marginal contacts are presumably normal, i.e. they are overlapped by the ventrolateral plates on all sides, except where they are in contact with one another.

The anterior ventrolateral plates (Pl. 26; Pl. 28, fig. 3; AVL, Text-figs. 3, 6, 7, 10) are remarkably tumid, or shell-like, and form a substantial part of the lateral wall with a very distinct lateral keel running backwards well above base level from the apex, which is presumably the growth centre, while two or three shallow grooves run forwards and inwards on to the interlateral. In front view (Text-figs. 6, 8) the basal part below the keel is convex, so convex that the anterior median ventral plate lies in a wide groove, whereas above the keel the lateral part is concave; but to the rear both curves become less pronounced (Text-fig. 12). Longitudinally the long basal portion behind the apex is gently convex, and again the short anterior part, which rises to the interlaterals, is concave.

The right anterior ventrolateral plate has slipped inwards slightly and shows by its entire margins that it overlapped the two median ventral plates and the front of the posterior ventrolateral: the left plate has the same form, apart from a slight healed injury near the PMV–PVL contact. The contact in front with the interlateral and with the spinal along the top (both presumably being sutured to or slightly

overlapped by it) is very close, for they have moved as one piece with the anterior ventrolateral and the anterior lateral. In side view (Text-figs. 2, 7) the margin with the spinal is almost straight and continues straight behind it under the pectoral fenestra for half its length, and then turns sharply upwards to form a small triangular projection to meet the posterior lateral, closing the fenestra and cutting off the posterior ventrolateral from the margin.

The posterior ventrolaterals (Pl. 26; Pl. 27, fig. 2; PVL, Text-figs. 3, 4, 7, 10) are very dissimilar in shape ventrally, for the right plate widely and irregularly overlaps the left instead of, as seem more usual, the left moderately and regularly overlapping the right. In side view the ventral face of each plate at first continues the curve of the anterior plate, so that the general longitudinal basal profile is markedly convex. The main ventrolateral keel is very faint in front of the centre of the plate, so that the plate is at first rounded in cross-section, but thereafter the keel is strongly developed with a complementary groove over it, sharply dividing the side from the undersurface, both of which become flattened and lie almost at right angles to one another. The anterior margin of each plate is strongly embayed by the overlap of the plate in front, but at the top of the indentation the margin turns at right angles to run vertically for a short distance against the anterior ventrolateral prominence. The dorsal margin, in contact apparently by suture with the posterior lateral, is sigmoidal, being at first slightly concave and then broadly convex as far as the hinder margin which it meets at a wide angle. The free hinder margin sweeps down and backwards in a deep hollow curve to meet the ventrolateral keel at a very acute angle, so that the length of the plate dorsally is only about two-thirds or less of its maximum (ventral) length.

The interlateral plates (Pls. 26, 27; Pl. 28, fig. 3; IL, Text-figs, 3, 4, 6–8, 10) apparently face wholly forwards and downwards, for above they seem to be sutured to the apron of the anterior laterals along the front edge of the armour, forming a very prominent denticulated keel, largely abraded in this specimen, passing into that of the spinal. They meet one another in the midline along a minute vertical facet, and below they are firmly attached for a short distance to the anterior median ventral (where they are narrowed by the convex front margin of that plate) and to the anterior ventrolateral as far as the rounded anterior lateral corner where each side is closely sutured to the corresponding spinal plate.

The spinals (Pl. 26; Pl. 27, fig. 1; Pl. 28, fig. 3; SP, Text-figs. 3, 5–10, 13a), forming the main lateral keels, curve gently backwards to the pectoral socket of which they form the anterior, partly transverse margin, but without formation of a spine. These plates are bluntly triangular in section (Text-fig. 13a) since, unlike the interlaterals, they have a large, gently convex upper surface which meets the lower edge of the anterior laterals at a wide concave angle.

The anterior lateral plates are very remarkable (Pl. 26, fig. 2; Pl. 27; Pl. 28, figs, 1, 3; AL, ALA, Text-figs. 3–10). High and wide with a strong keel about a third of the way up the side, they have an extremely broad mesial lamina or apron (ALA) in front at right-angles to the lateral face. The apron, which has a peculiar ornamentation of its own (see p. 265), slopes in a gentle hollow curve upwards and backwards very nearly at 45° to the line of the spinal plate. Transversely it was also
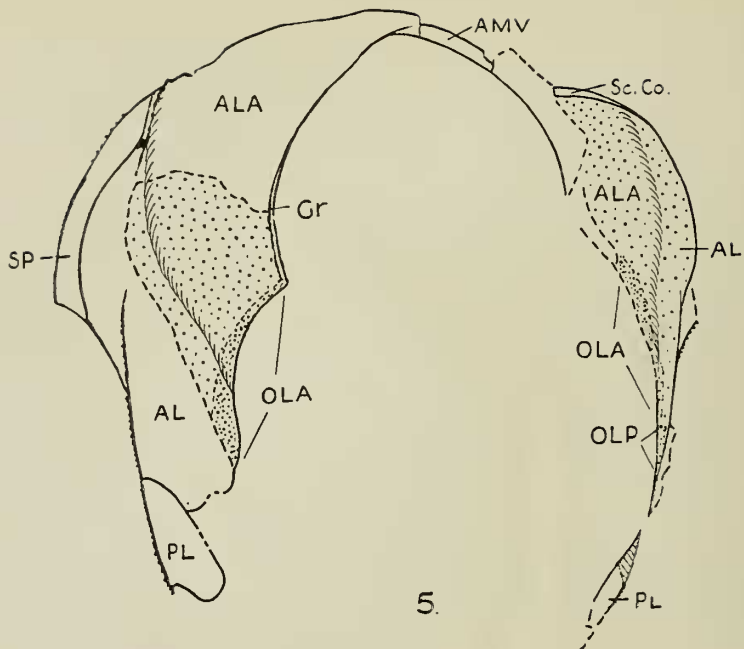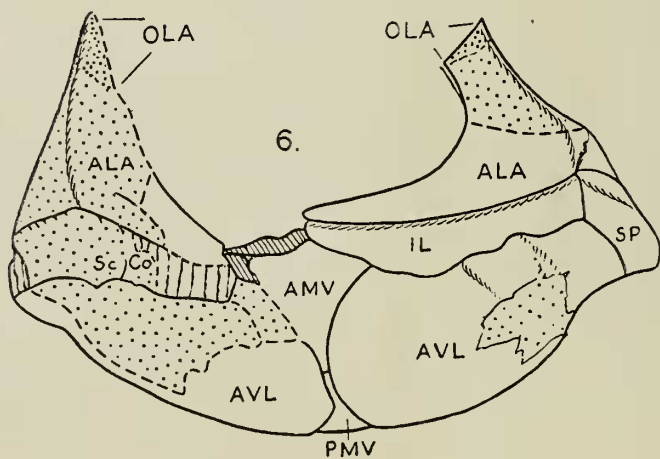
Williamsaspis bedfordi gen. et sp. nov.

TEXT-FIG. 5. Outline of body-armour in antero-dorsal view. The holotype, P.27073, × 1½ approx.

TEXT-FIG. 6. The same, front view, slightly uptilted, × 1½ approx. Shading &c. as in Text-fig. 4.

(For explanation of lettering see pp. 303–304.)

slightly concave. The mesial margin is deeply embayed, forming almost the quadrant of a circle, but is at the same time slightly sinuous. The free edge is smoothly rounded upwards in the lower half, but about half-way a groove (Pl. 28, fig. 1; Gr, Text-figs. 5, 8, 9) comes from the undersurface on to the free edge itself, finally facing partly upwards along the margin. As noted above, the division between the apron and the interlateral plate seems to be along the line of the ridge, continuing the suture between the lateral face and the spinal, but no suture can be detected externally and only a suggestion of such internally in broken cross-sections, the two plates being fused together. The angle between the apron and the lateral face (AL) of the anterior lateral is virtually a right angle, rounded off on the inner surface shown on the internal cast, but the bone itself is only preserved at the lower front end where a sharp ridge dividing the two surfaces is actually present and may continue to the top. The lateral face is roughly trapezoidal, except for a large triangular posterior process bearing the keel and overlapping the posterior lateral, for the rounded top margin is shortened by the slope of the apron and the lower margin cut off by the pectoral opening.

The posterior laterals are equally curious in form, being elbow-shaped (Pl. 26, fig. 2; Pl. 27, fig. 2; PL, Text-figs. 4, 7). Each has a narrow lower shank running steeply below the anterior lateral process down to the pectoral opening, of which it forms the concave posterodorsal border, and a wider upper shank with a rounded dorsal border passing into a gently concave free posterior margin. The latter slopes backwards and downwards, forming a very acute angle with the sigmoid lower margin, which in front has a very small contact with the triangular process of the anterior ventrolateral. The keel of the anterior lateral plate is continued, at first faintly (in part due to abrasion) and then strongly to the point of the posterior angle. The curious external shape of this plate is due to the strong triangular overlap of the anterior lateral, but even when isolated it is still very irregular in outline (Text-fig. 11) with its fan-shaped overlapped area.

All the dorsolateral plates and the median dorsal had become loosened and disappeared before fossilization, but we know a little about both the anterior and posterior dorsolaterals from the extent of the overlapping areas on the anterior lateral (OLA, OLP, Text-figs. 4–6). The area overlapping the anterior dorsolateral runs forwards along two-thirds of the upper lateral margin of the anterior lateral plate, continuing as a narrow and decreasing selvage to the mesial margin of the apron, so that the anterior dorsolaterals also had a transverse flange that formed the top of the apron. The extent of the posterior dorsolateral is not so certain, but presumably its hinder margin continued the curve of the posterior lateral. A possible restoration of the missing plates is given in Text-figs. 7, 8. If the anterior dorsolateral plate bore an articular peg, as it does in most arthrodires, and not just an overlapped flange, such as Stensiö (1944: text-figs. 17a; 1945: 7) records in *Kujdanowiaspis*, the median dorsal plate must have been at least as high as shown to allow for the depth of the skull, since the median articulations at the base of the skull must, of course, be in line with the external pair on the armour to allow the head to swing. But in view of the rapid narrowing of the armour upwards, both laterally and transversely, the level of the back was probably not much higher. If the restoration is
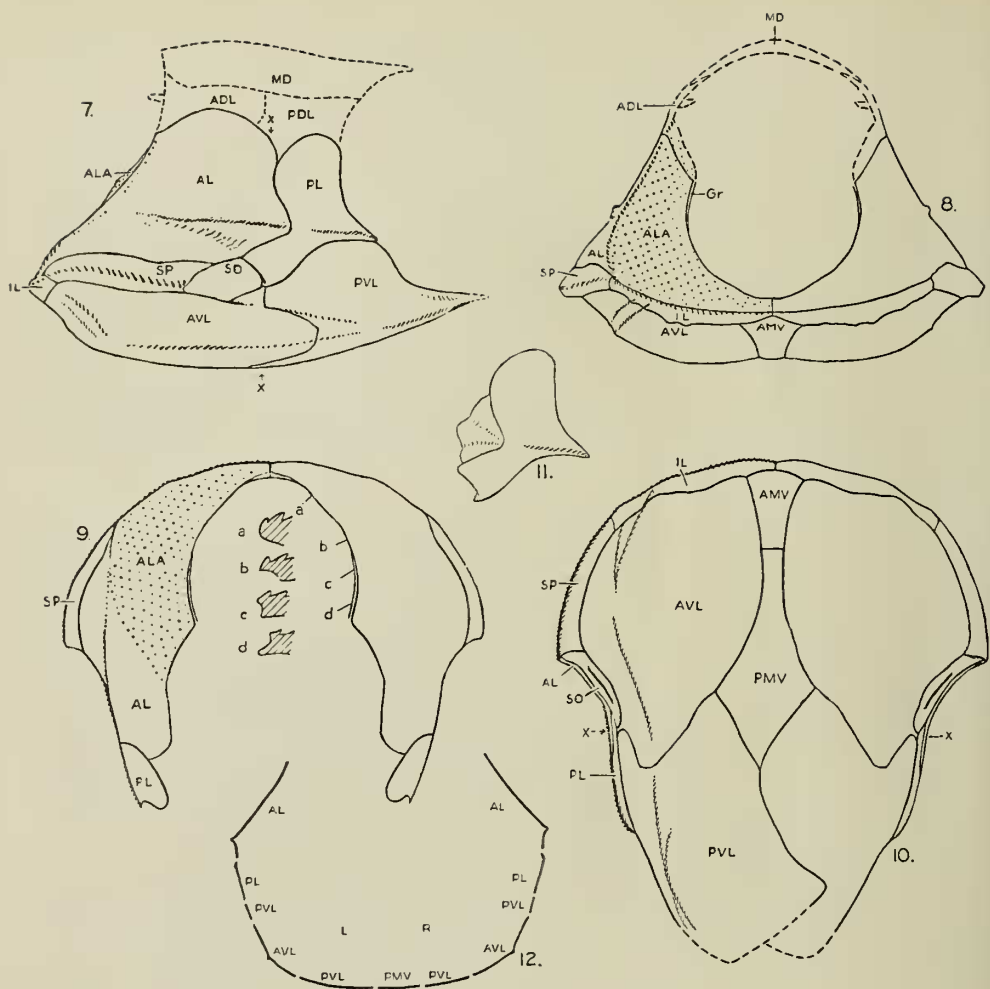
Williamsaspis bedfordi gen. et sp. nov.

TEXT-FIGS. 7–10. Restorations in outline of body-armour: (Fig. 7) direct side view; (Fig. 8) front view, tilted slightly forwards; (Fig. 9) in antero-dorsal view, at right angles to the apron, with cross-sections of free inner edge (*a–d*); and (Fig. 10) ventral view. The left sides of Figs. 8–10 show the ridges, the right sides outlines only. Area of anterior lateral apron stippled. Approx. nat. size.

TEXT-FIG. 11. Restoration in outline of left posterior lateral plate showing area overlapped by anterior lateral plate. Approx. nat. size.

TEXT-FIG. 12. Cross-profile at *X–X* in FIGS. 7 and 10.

(For explanation of lettering see pp. 303–304.)

approximately correct, then the relatively high position of the hinges does give, subject to the limiting factor of the size of the gap between the nuchal and median dorsal plates, a wide arc of possible movement to the head which would require an extremely flexible throat. It also means a relatively large branchial chamber, and where this feature is marked, as in the 'monaspids' (Heintz, 1929: text-fig. 9), the ptyctodonts (Watson, 1938: text-fig. 3), *Williamsaspis*, and rather less so in *Palaeacanthaspis* (Stensiö, 1944: text-fig. 3), the anterior lateral apron is also conspicuous. To that extent there is some correlation between these two features, but they are not proportionately developed.

The form of the scapulo-coracoid can be accurately determined from the complete interlateral and spinal plates of the left side and the impression of the girdle on the internal cast shown on the fractured right side (Pl. 27; Pl. 28, fig. 3; Sc Co, Text-figs. 3–6, 13–15, 17, 18), where in places part of the relatively thick perichondrial bone with which it was invested is preserved. Seen from above or below it is very similar in form to that shown in Stensiö's (1944: text-fig. 17B) restoration of *Kujdanow-iaspis* and is presumably that of a typical arctolepid (Text-fig. 13). The scapulo-coracoid runs from the front midline, where the coracoid process is separated from its fellow only by the minute median wall of the containing interlateral, backwards in a gentle curve to the hinder edge of the pectoral socket behind. It widens steadily from the midline of the body to about two-thirds of the distance to the anterior lateral corner and then narrows sharply, forming a distinct inner angle, the anterior mesian angle (AMA, Text-fig. 13). After passing laterally under the spinal plate it gently widens again to the front of the socket where it forms a slightly obtuse external angle but no spine, and behind which it forms a wedge, with a long concave posterolateral outer face fitting the pectoral socket. In cross-section (Text-fig. 13a) the cartilage is roughly triangular, following the shape of the spinal keel, with the inner surface mostly convex, but slightly sinuous and facing somewhat upwards. The outer surfaces meet at an angle of about 60°, the lower being nearly horizontal. The perichondrial bone is preserved in a number of places and evidently invested the whole cartilage and lined the foramina in it. It is fused along the outer faces with the investing dermal bones; in front it has only the apron above and the interlateral and the anterior ventrolateral below, but along the sides the spinal covers the whole of both external surfaces, with only narrow selvages under the anterior lateral above and the anterior ventrolateral below.

In front view (Pl. 28, fig. 3; Text-figs. 6, 14, 18) the coracoid process seems to have tapered mesially (distally), although this part is not preserved in the fractured right side, but its shape can be roughly determined from the form of the enveloping interlateral on the left side. It increases gradually in depth towards the sides, rising steadily as it approaches the spinal margin, where it immediately straightens out and passes levelly under the spinal plate as far as the pectoral fenestra. There it turns up to fit under the socket, wedging out at the margins, so that the form of the socket face is preserved by the perichondrial bone layer. The lateral, scapular part of the cartilage is of even depth (Pl. 27, fig. 2; Text-figs. 4, 15, 17) with no scapular process, but the whole impression of the upper margin on the anterior lateral is pinked where the dorsal neurovascular canals passed over the upper edge of the
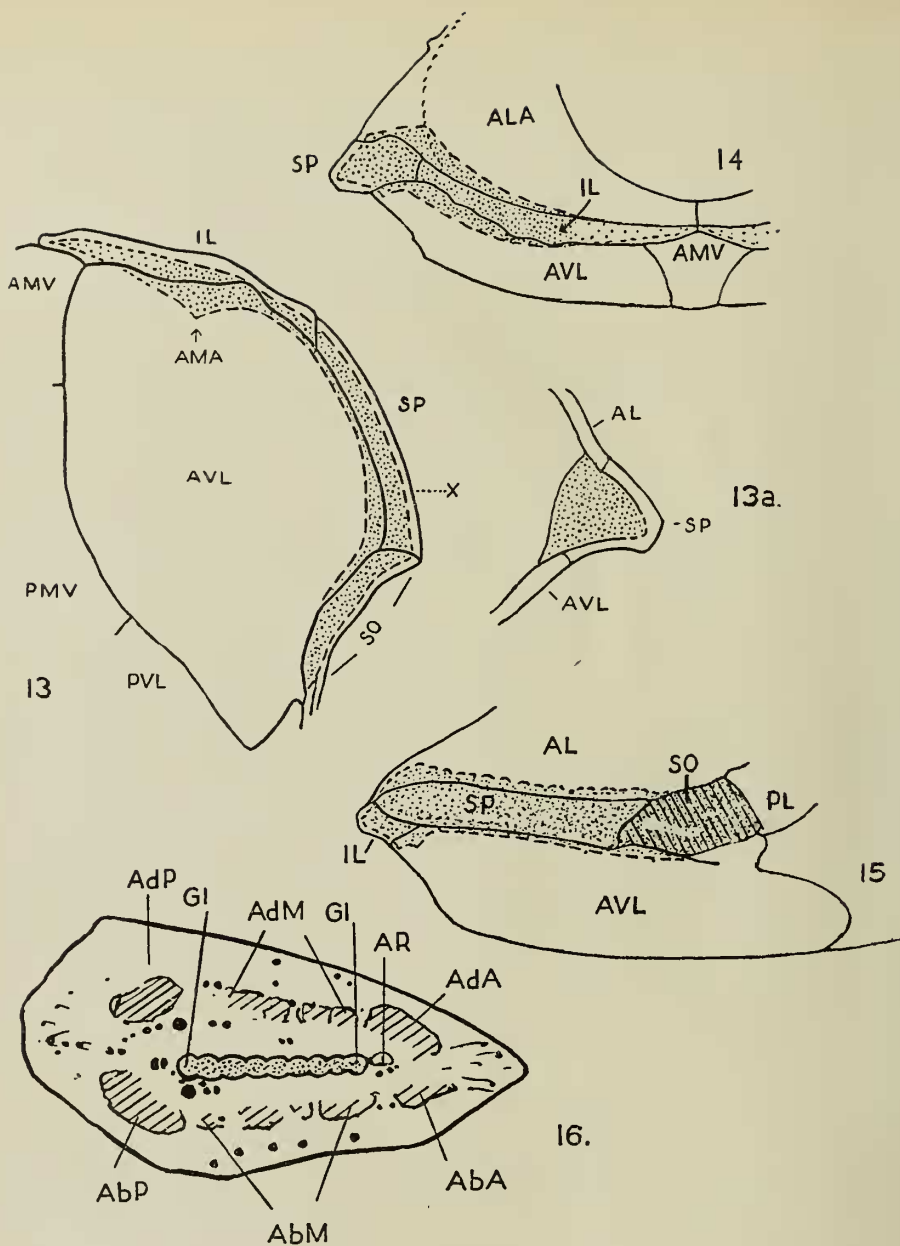
Williamsaspis bedfordi gen. et sp. nov.

TEXT-FIGS. 13–15. Restorations in outline of the forequarter of carapace to show form of the scapulo-coracoid (stippled with pectoral fenestra shaded): (Fig. 13) from below with (13a) enlarged cross-section at X; (Fig. 14) from the front; (Fig. 15) from the side. $\times 1\frac{1}{2}$ approx.

TEXT-FIG. 16. Restoration in outline of right pectoral fenestra flattened out. Cartilage stippled; muscle attachment-areas diagonally shaded; neuro-vascular foramina black. $\times 4\frac{1}{2}$ approx.

(For explanation of lettering see pp. 303–304.)

scapulo-coracoid and down the dorsolateral outer face. There are indications of over twenty of the dorsal vessels from a little in front of the fin-socket as far forward and mesially as the right side is preserved, i.e. about two-thirds of the way along the inter-lateral border. The notches are not absolutely regularly disposed: in front (Text-fig. 18) the notching is much deeper and more oblique, the canals forming strong ridges on the perichondrial layer of the mesial face which finally overlap the ventral series; behind, near the fin-socket, one or two of both dorsal and ventral series actually passed through the cartilage itself as the bony tubes show, instead of between the dermal basal layer and the perichondrial layer. The passage of the ventral series is not so clearly marked as the upper, these canals passing under the cartilage without deeply notching it.

The exposed surface of the scapulo-coracoid is completely surrounded by plates forming a conspicuous pectoral fenestra (Pl. 26, fig. 2; Pl. 27, fig. 2; Pl. 29; SO, Text-figs. 3, 4, 7, 10, 15–17, 19). It is bordered by the spinal plate in front, the laterals above and behind, and the anterior ventrolateral alone below, for this last plate sends up a small triangular projection to meet the posterior lateral and so completely excludes the posterior ventrolateral plate from the fenestral margin. It measures approximately 1·5 cm. in length when flattened, or about two-ninths of the maximum length of the body-armour, but appears to be much shorter owing to its concave face and partly diagonal position (Pl. 26, fig. 2). The face is not vertical but directed slightly downwards (Pl. 26, fig. 1; Text-fig. 10). In outline (Text-fig. 16) it forms a rough unequal-sided pentagon with a long dorsal margin sloping downwards, so that it is more pointed and shallower in front than behind. The surface is completely covered with a thin layer of perichondrial bone except for the actual articular surface of the basals, which was unossified (Text-fig. 16, Gl–Gl). The bone is, of course, continuous with the similar bone encasing the rest of the scapulo-coracoid cartilage which is fused with the basal layers of the neighbouring dermal bones except apparently that of the posterior lateral behind where, owing to the fine wedging out of the contained scapular cartilage, the outer perichondrial lamina meets the inner in a free knife-edge. On the right side where all the anterior plates have become slightly detached, the fenestral cover has moved as one piece with them and shows an unbroken dorso-posterior margin (Pl. 29, fig. 1; Text-fig. 17). The most conspicuous feature of the exposed surface is the long slit which in life was occupied by the cartilaginous articular surface of the pectoral basals. Only on the right side (Pl. 29, fig. 1) is part of the actual edge of the bone surrounding the articular area preserved, along the front half of the upper margin and the anterior end. The margin is slightly raised so that the articular surface was in the form of a low narrow ridge, and from the five faint more or less equal crenulations preserved we may estimate that there were some nine separate basals. Immediately in front, isolated but in contact, is a much narrower bony cup (AR, Text-figs. 16, 17) which may be for the direct attachment of the anterior and perhaps spinous, fin-ray. It has a faint median vertical ridge.

The muscle-scars are very clearly shown and are remarkably symmetrical about the articular ridge. On each side the musculature was divided into three parts—a wide shallow depression in front, a median series of roughened areas cut up by
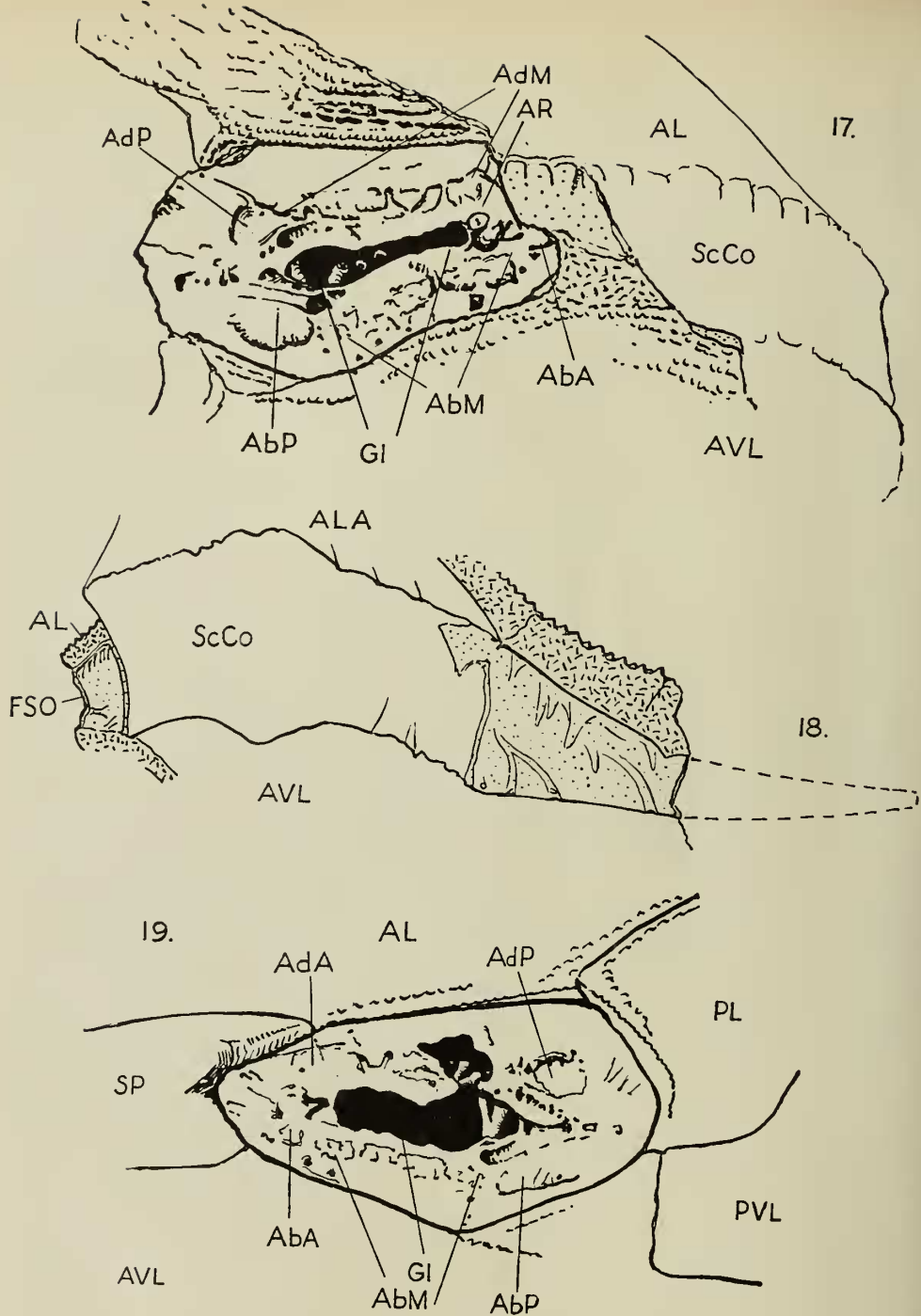
Williamsaspis bedfordi gen. et sp. nov.

TEXT-FIG. 17. Right pectoral socket and internal impression of scapulo-coracoid in side view, *cf.* Pl. 29, fig. 1. The holotype, P.27073, ×4½.

TEXT-FIG. 18. Front view of right scapulo-coracoid of same specimen showing either the internal impression (plain) or the medial perichondrial cartilage (dotted). Broken surfaces of plates are long stippled. *Cf.* Pl. 28, fig. 2. ×3½ approx.

TEXT-FIG. 19. Left pectoral socket of same specimen, *cf.* Pl. 29, fig. 2. ×4½.

(For explanation of lettering see pp. 303–304.)

vascular grooves, and still wider shallow areas behind, the only marked difference between the adductor (dorsal) series and the abductor (ventral) series being that the dorsal posterior and the ventral anterior areas are somewhat smaller than their opposites.

In this fish all the vessels and nerves supplying the fin must, of course, come through the girdle and pass out through the limited surface of the pectoral fenestra. Apart perhaps from some of the finest when filled with matrix, the foramina are easily recognized in the perichondrial bone (Pl. 29, Text-figs. 16, 17, 19) and the ossified tubes of some of the larger vessels may be seen through the articular slit, especially on the left side where the margins are most extensively broken. It is not possible to assign to these irregularly distributed foramina their precise functions, but the important vessels are concentrated largely at the hinder end of the articular ridge—one particularly large and one double foramen below, a double foramen behind, and a very large opening above. These doubtless carried the nerves of the brachial plexus and branches of the subclavian artery and vein to both dorsal and ventral sides of the fin. The small foramina provided passage for the dorsal and ventral branches of the cutaneous arteries, veins, and nerves, and almost all lie at the end of grooves directed towards the articular ridge.

The ornamentation of the plates consists for the most part of well-separated lines of closely packed stellate tubercles (Pls. 26–29; Text-figs. 1, 2) disposed roughly parallel with the margins of the plates, and is rather like that on certain plates, such as the anterior lateral, of *Phlyctaenaspis*, except that the lines are finer and the tubercles (Pl. 28, fig. 2) more coarsely stellate. The valleys between are finely crinkled and owing to the thinness of the external layer the tubules of the spongiosa are frequently seen. Near the centre of the larger plates the tubercles are more irregularly disposed and on the longitudinal ridges or keels closely massed, especially on the spinal-interlateral keel where they are slightly, but only slightly, enlarged. The only exception to this type of ornamentation is on the apron of the anterior lateral plate which is covered with sharply pointed, depressed triangular pyramids (Pl. 27, fig. 1; Pl. 28, fig. 1). These are directed forwards or antero-laterally with the large, flat upper face showing as a rule three ridges, one median and one along each side, meeting at the apex of the triangle. How clearly the ornamentation of the apron was marked off from that of the side is not certain, as the bone of the angle between is lost except at the very front bottom corner, and here they are separated by a ridge.

One interesting point about the ornamentation of the apron in this particular specimen is that along the lower outer margin near the angle between the two faces an area has been cleared of its original coarse ornament and this has later been replaced by a few scattered and very small tubercles of the same design as the larger originals. Whether this defect is due to accident or disease is not certain, but the final result is very like that of the obvious bites seen on the skull-roof of another genus (see p. 271 *infra*).

REMARKS. *Williamsaspis* presents a number of peculiar features which isolate it systematically. Its well-developed armour with the large spinal plate show its arctolepid affinities, but so far as I know it is the only arthrodire with a well-rounded undersurface and the spinal plate consequently placed well up the side. *Euryaspis*,

it is true (Bryant, 1934: 139), has the anterior ventrolateral plates 'arched very gently from side to side in front', but it has a conspicuous lateral spine, while in the very different *Palaeacanthaspis* (Stensiö, 1944: text-figs. 3, 4) the same plates form a small part of the lateral surface but the much reduced ventral armour is flat and there again a lateral spine is present. Except for the laterally compressed genera from Wildungen (Oxyosteidae, Synaucheniidae, Gross, 1932:39, text-figs. 17–25), arthrodires seem to have had flat bottoms. But it is the undeveloped condition of the lateral spine on the large spinal plate that is so characteristic of *Williamsaspis* and with it goes the evidence of well-developed pectoral fins provided by the pectoral fenestra and the seating of the fins. The absence of a large pectoral spine is, I think, also an unspecialized character, due to non-development rather than loss. But the curious elbow-shaped posterior lateral plates, which forms a large arc of the margin of the pectoral fenestra, is a more original development, so far unknown in other arthrodire genera, while the extreme development of the apron of the anterior lateral plate still further sets it apart from other arctolepids.

By and large it seems most appropriate to treat *Williamsaspis* as the only member of a special group of arctolepids, characterized by the undeveloped pectoral spine, its peculiar pectoral fin, large apron, rounded undersurface, and possibly also the elbow-shaped posterior lateral plate.

Order *COCCOSTEIFORMES*
Sub-Order BRACHYTHORACIDI
Family BUCHANOSTEIDAE

DIAGNOSIS. Broad-headed brachythoracids with long nuchal-paranuchal region and short wide central plates. Ventral surface of neurocranium, vessels, and cranial cavity invested with perichondrial bone, the post-ethmoid region probably ossified in a single piece, with wide suborbital shelves, shallow and broadest at base in cross-section between the two postorbital processes; posterior process single, pierced by large vein. Occipital region wide and extremely short.

REMARKS. There seems little point in extending the diagnosis in view of our limited knowledge of this form and of the corresponding parts in other brachythoracids.

Genus *BUCHANOSTEUS* Stensiö, 1945

DIAGNOSIS. As for family (only genus).

REMARKS. The genus *Buchanosteus* was proposed by Stensiö (1945: 8, 24) for the arthrodire described by Hills (1936) as *Coccosteus osseus* on the grounds that the endocranial structures shown by the holotype resembled those of a dolichothoracid (arctolepid) and differed apparently very widely from such structures as were known among brachythoracids. However, specimen P.27071, which is surely congeneric with Hills's, displays a number of new features that in my opinion show that Hills was undoubtedly right in so far as he interpreted his fossil as a brachythoracid (see pp. 274–6 *infra*), and at the same time it adds very materially to our knowledge of the endocranial structures of the group.

The form of the skull-roof, the position of the eyes, and the pattern of the plates composing the roof and of the sensory canal system clearly stamp these fishes as brachythoracids—in particular we may note the relationships of the eyes to the pre-orbitals, the wide-based nuchal, the short occipital region, and the absence, as shown by the sensory canals, of lateral extrascapular elements in the paranuchals, the last a point on which Stensiö (1945: 42, 48, 55) has laid some emphasis.

GENOTYPE. *B. confertituberculatus.*

Since by common practice varietal names have the same standing as those of sub-species (cf. *Int. Rules Zool. Nomen.*, 1926, art. 12), Hills's specific epithet *osseus* should not be used. His holotype is also the holotype of Chapman's (1916: 213) *Phlyctaenaspis australis* var. *confertituberculata*, and as it is apparently impossible to say whether this specimen is conspecific with the types of McCoy's still earlier *Asterolepis ornata* var. *australis* (Hills, 1936: 214), Chapman's varietal name must stand for the species. The name of the genotype is therefore *Buchanosteus confertituberculatus* (Chapman).

Buchanosteus murrumbidgeensis sp. nov.

(PL. 30; PL. 31, FIGS. 1, 2; TEXT-FIGS. 20–27)

DIAGNOSIS. A *Buchanosteus* with long antero-lateral (postorbital) margin of skull-roof and short postero-lateral margins. 'Preopercular' sensory groove very short. Ornamentation of dermal bones consisting of numerous irregularly arranged tubercles capped with numerous fine radiating ridges and having a smooth waist passing below into coarse irregularly radiating ridges.

MATERIAL. The holotype (a diagonal slice of the skull, P.27071) and a fragment of the median dorsal plate of a smaller individual, P.27072.

FORMATION AND LOCALITY. Middle Devonian: Parish of Taemas, Murrumbidgee River, N.S.W.

DESCRIPTION. The holotype belongs to a much larger individual than that of *B. confertituberculatus*, if Chapman's (1916: 213) original dimensions and not Hills's (1936: expl. pl. iii) magnification is correct; for Chapman gives the approximate width of his fossil as 69 mm., whereas the new fragment represents a skull about 125 mm. over the curve at the paranuchals. This specimen, being diagonally cut (Pl. 30, fig. 1; Text-fig. 20), shows part of all the component plates of the skull-roof except the rostral and the postmarginal, and a very fair reconstruction of the roof may be made (Text-fig. 21). The whole of the anterior and most of the posterior margins are missing, as are also the preorbital and postorbital processes. The individual bones are strongly fused together, but in the hinder part the sutures are clear enough; elsewhere they are less certain owing to the dense ornamentation, cracks, and the scars due to injuries received during the lifetime of the animal.

The specimen has been carefully developed in acetic acid in an effort to clear the internal structure, but the ossification is so very light that the process had to be stopped before completion to avoid serious damage to the specimen (Text-fig. 22).

The skull-roof has a perfectly straight median longitudinal profile so far as it is preserved, and transversely is flattened on top but strongly curved downwards at the

sides (Text-figs. 23, 24). Except for the small postmarginal plate, which has not been detected, the right lateral margin is complete, including the lateral-posterior corner and as far forwards as the postorbital prominence. On the left side part of the upper margin of the orbit is preserved.

The whole surface is closely covered with small tubercles, most of which have been worn smooth or damaged during the lifetime of the fish. However, a substantial proportion are intact (Pl. 30, fig. 2) and show that the caps of the tubercles were
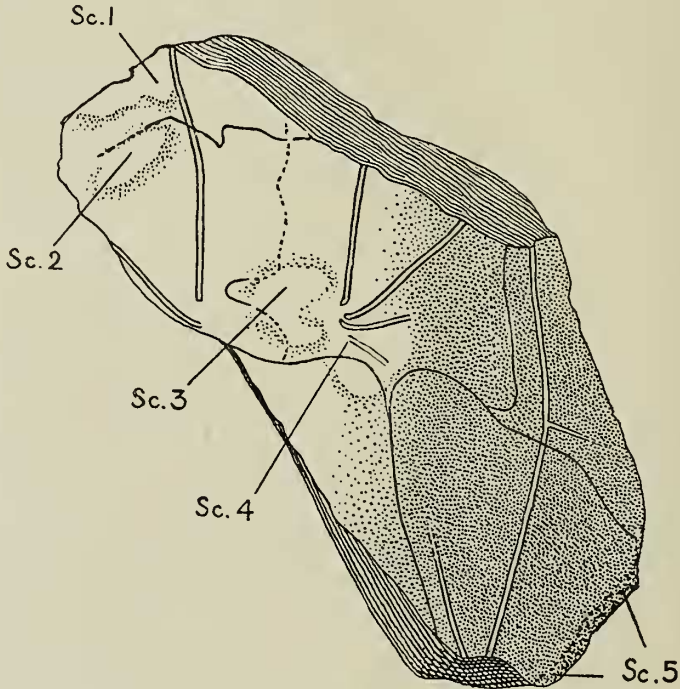
Buchanosteus murrumbidgeensis sp. nov.

TEXT-FIG. 20. Diagonal slice of skull-roof, original condition with fractures omitted, but showing scars (Sc. 1–5). The holotype, P.27071, nat. size.

domed or bulb-shaped and covered with numerous fine radiating ridges. Below the cap there is a slight, smooth waist which passes into the base formed of up to twenty coarse irregularly radiating and almost smooth ridges like the roots of ancient trees. These ridges coalesce with those of neighbouring tubercles to form a coarse network on the intertubercular spaces, in the meshes of which open conspicuous external pores from the middle layer.

The crude microstructure of the bone is readily seen in the fractured surfaces and corresponds well enough with the descriptions of Heintz (1929: 27, fig. 5, pls. xxii–xxiv for monaspids) and Gross (1930: 135, pl. ii, figs. 10, 12, 13; 1935: 25, for *Coccosteus*). Heintz divides the bone into four layers (basal, canal, reticular, and surface),

Gross into three (basal, spongiosa, and tubercular), both emphasizing the gradual transition between one layer and the next. Everywhere in this specimen the surface layer is extremely thin in the intertubercular spaces where the external pores are conspicuous, but it forms the whole of the caps of the tubercles, appearing as a dark, dense substance without any visible perforations. The spongiosa forms practically the whole thickness of the bone, for a lamellated basal layer does not seem to be developed except for a single very thin sheet indistinguishable from the perichondrial bone of the endocranium with which it appears to be continuous. The spongiosa varies in texture and thickness from place to place. Sometimes, as in the flat middle part of the head near the pineal region where the bone is thin, a lower *canal zone* and an upper *reticular zone* may be distinguished, while farther back the thick bone of the nuchal plate shows a thin horizontal cavity which tends to split the upper part in two. Near the front of the central plate, at the start of the downward curve, the lowest part encloses some relatively large vessels, some of which are seen below as discrete tubes of perichondrial bone where they passed upwards through the unossified endocranium (*cf.* cutaneous vessels; Stensiö, 1945: text-fig. 1). On the sides of the head the bone again thins somewhat before passing into the thick marginal area where the whole of the spongiosa is uniformly trabecular, with gradual and relatively slight decrease in size of mesh from bottom to top. But below large vessels seem to be adhering to the roof. A remarkable feature shown by the skull-roof is that in places the thin outer tubercular surface layer has been formed as skin without any spongiosa over a similar layer with smaller tubercles, which may be readily exposed by simply chipping the outer layer away (Pl. 30, fig. 3). That this is an abnormal development seems probable, but so far as I am aware no account of the means of growth of arthrodire plates has been published.[1] For that matter, no remains of really juvenile arthrodires have been described, the smallest being about half-grown (cf. Watson, 1934: 442), but even these are very rare, so that a true growth-series is not available. Since the tubercles of the ornamentation appear to increase with size and the thickness of the surface layer does not, this layer was possibly normally resorbed and redeposited. The battered condition of this piece of skull suggests that the fish may have been very old, and the apparent physiological lapse suggested by this abnormal growth due to senility.

The outlines of the component bones are given in Text-fig. 20 and the whole restored in Text-fig. 21. The form of the bones at the back is perfectly clear, and most of the others may be accepted with some confidence. The very large nuchal is trapezoid and slightly concave in front, the equally large paranuchals broadly triangular and diagonal, the centrals very short and wide, but the sutures with the postorbital are the least satisfactory. The posterior and posterior orbital margins are restored from Hills's (1936: text-fig. 6) reconstruction of *B. confertituberculatus*.

The skull-roof is deeply incised by the grooves of the sensory canals, which closely resemble in their distribution those of coccosteids (e.g. Stensiö, 1925: figs. 24*a*, *b*), particularly of *C. decipiens* as figured by Heintz (1931*a*: 295, fig. 3). On each side the groove of the supraorbital canal (*soc*) runs forward from the posterior-mesial area

[1] However, Dr. T. Ørvig kindly informs me that he considers that this is the normal method of growth in the arthrodire exoskeleton.

of the central plate, diverging from its fellow as it passes on to the preorbital. A little farther back from the same spot (which is presumably the centre of ossification of the central plates, although this cannot be seen) the central sensory groove (*csg*)
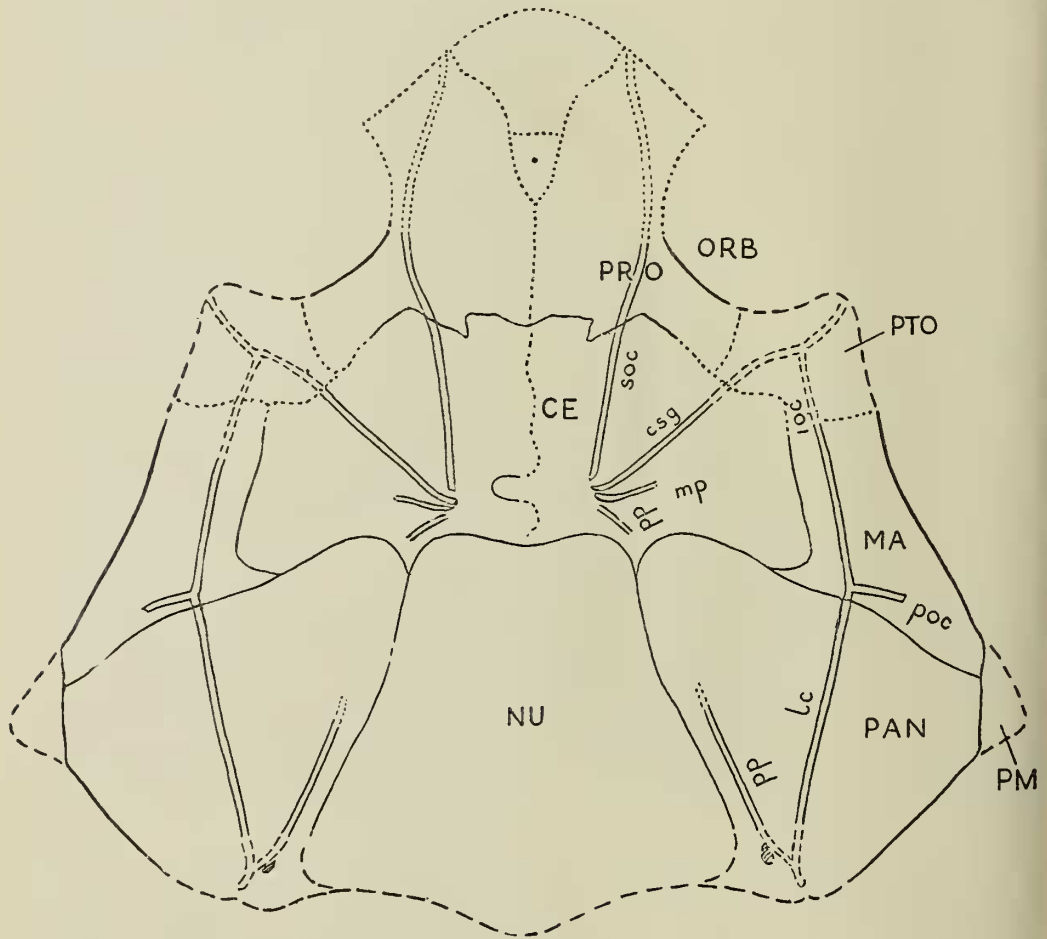
Buchanosteus murrumbidgeensis sp. nov.

TEXT-FIG. 21. Restoration of skull-roof flattened out, based on holotype, P.27071. Parts based on Hill's (1936) specimen of genotype shown by broken lines. Nat. size.

(For explanation of lettering see pp. 303–304.)

passes obliquely forwards and outwards towards the postorbital plate, where doubtless it joined the infraorbital groove (*ioc*). This groove is seen to run backwards over the margin to continue as the main lateral line groove (*lc*) to the postero-median border of the paranuchal plate, giving off in the process a short preopercular groove (*poc*) a little in front of the hinder border of the marginal plate.

A third groove on the central plate is that of the short transverse median pit-line groove (*mp*), and there was yet a fourth, the groove of the anterior part of the posterior pit-line (*pp*), as in Stensiö's restorations of *Coccosteus* (1925: 174, fig. 24*a*) and *Kujdanowiaspis* (1945: 34, fig. 8). This part is almost obliterated by scarring, but the groove of the posterior part of this pit-line clearly runs forwards from the posterior end of the main line (with which it was undoubtedly joined) alongside the nuchal plate fading out at about the middle of its length.

Not the least interesting point about this specimen is the scarring of the roof-bones, due to wounds received either in fighting, or more likely in predatory attack. Immediately above the left orbit, where the preorbital, postorbital, and central plates should meet, there is evidence of damage of two kinds, gouging and shearing (Pl. 30, fig. 1). On the preorbital plate the spongiosa has been gouged out and then repaired most incompletely and irregularly, sometimes by regrowth of the spongiosa, apparently without the surface layer and to the extent of making a slight bump above the normal surface, while over most of the affected area the depression in the spongiosa has not been filled in, but instead scattered, fully formed tubercles of the surface layer cover the rough surface of the depression (Text-fig. 20; Sc. 1). The hinder part of this area has been sheared off at a later date since the damage appears to affect the previous repairs, while a similar slicing wound on the neighbouring area of the central plate ends in a clear straight cut (Sc. 2).

In the centre of the skull-roof (Pl. 31, fig. 2), on the hinder part of the suture between the central plates, is evidence of larger wounds. The earlier is again a gouged pit which has been imperfectly repaired (Sc. 3), partly by a thin covering of the external glassy layer with scattered tubercles and partly by secondary deposition of spongiosa, which further formed an irregularly raised rim around the hole, but on the right side, where the four grooves converge, the primary ornament has again been planed off and with it the secondary rim of the original wound (Sc. 4). The paranuchal border is also planed off (Sc. 5).

The earlier set were gouged out by powerful pointed teeth belonging to a creature that was certainly a good deal larger than its victim. It is not the sort of wound that one would expect from an arthropod (or any other invertebrate, however large) and may be considered certainly due to the bite of a vertebrate predator, i.e. another fish. Contemporary sharks, palaeoniscoids and acanthodians are not known from these beds as yet and in any case would, unless they were excessively big, have inflicted a different type of injury giving a more linear scar; *Dipnorhynchus* (Hills, 1941) presumably had the usual dipnoan crushing dentition and could hardly have this effect; but the anterior prehensile tooth-plates of a large coccostean with a dentition like that of *Dinichthys* is just the right instrument and the two holes suggest that our creature was held diagonally across the head by the widely separated gnathals (see Heintz, 1932: 191, fig. 81; Watson, 1934: text-figs. 3, 4). How it managed to get away is another story, but that it did is evident enough from the repairs.

The second set of markings was obviously considerably later in age, since the first set had by then completely healed, and as they show no signs of repair they may have been made at the time of death, although in themselves not serious enough to have been fatal, or they may have been made *post mortem*, and Sc. 4 may even be an

artifact. If contemporary, it is not quite so clear what kind of teeth rasped these patches, but the cut which bounds the orbital wound (Sc. 2) suggests that they were the result of lateral movement by a blade, possibly by the victim struggling to free itself when caught by the posterior superognathals of yet another arthrodire. The only large contemporary arthrodire of which we have evidence is *Taemasosteus*, but although a good deal bigger than this fish, the specimen of which we have evidence was hardly big enough to have caused the first set of wounds, at any rate.

If some of these markings are indeed the result of attacks by other arthrodires, it certainly supports the idea that some arthrodires at least were active predators and not just carrion-feeders and conchophages (see Geuenich, 1939: 27; Stensiö & Jarvik, 1939: 266).

The undersurface of the fragment is most interesting since the base of the neurocranium was invested with a perichondrial bone-layer, which also lined the cavum cerebrale cranii and the canals of the vessels and nerves, as noted above. Unfortunately the part preserved is no more than the right posterior corner of the postethmoidal bone (Pl. 31, fig. 1; Text-figs. 22–24), from just behind the anterior postorbital process to the supravagal process; but with the holotype of *B. confertituberculatus* described by Hills (1936) one can obtain a fair general idea of the outline of the whole (Text-fig. 27).

The perichondrial bone lining the smaller canals is extremely thin, but that covering the undersurface of the postethmoidal bone is much thicker and shows a middle cellular layer. Laterally, above where the perichondrial bone meets the skull-roof, the spongiosa of the latter is thickened and contains one or more short longitudinal cavities (Text-fig. 23). The dermal skull-roof forms the roof of the shallow neurocranium, the thin basal layer being indistinguishable from the perichondrial bone with which it is continuous laterally. Owing to the investing bone the details of the side of the neurocranium between the two postorbital processes cannot be seen, but the front view, just behind the anterior process, shows it to be broader below than above, in distinct contrast to that of the arctolepid *Kujdanowiaspis* (Stensiö, 1945: text-figs. 4, 5). The undersurface is flat longitudinally (Text-fig. 24), the roof slopes on an even curve to the supravagal process, and there is no sign of a supranuchal depression. The neurocranium was deeply embayed between the two postorbital processes, but externally the covering bone runs evenly to the skull-roof, forming a rounded depression on which a number of clearly marked ridges run laterally outwards, possibly connected with the ligamentous attachment of the hyomandibula (*cf.* Stensiö, 1945: 22). The posterior postorbital process was single and carried the large vein (SHy) which certainly emptied into the jugular (VJu). Stensiö (1925: text-fig. 6) identified this vein in *Macropetalichthys* as the hyoid vein, but Holmgren (1942: 170) in his great work on the heads of fishes criticized this identification on the grounds that in sharks the hyoid vein enters the jugular farther behind the postorbital process and moreover the jugular itself is never enclosed in a canal in the cranial wall proper. He suggested that this vein and Stensiö's jugular form the v. subpostorbitalis. More recently in *Kujdanowiaspis* Stensiö (1945: 32, text-fig. 6, &c.) named this vein the 'v. posthyoidea lateralis', coming from the posterior dorsal parts of the cheek, and placed the hyoid vein still farther forwards in an even more
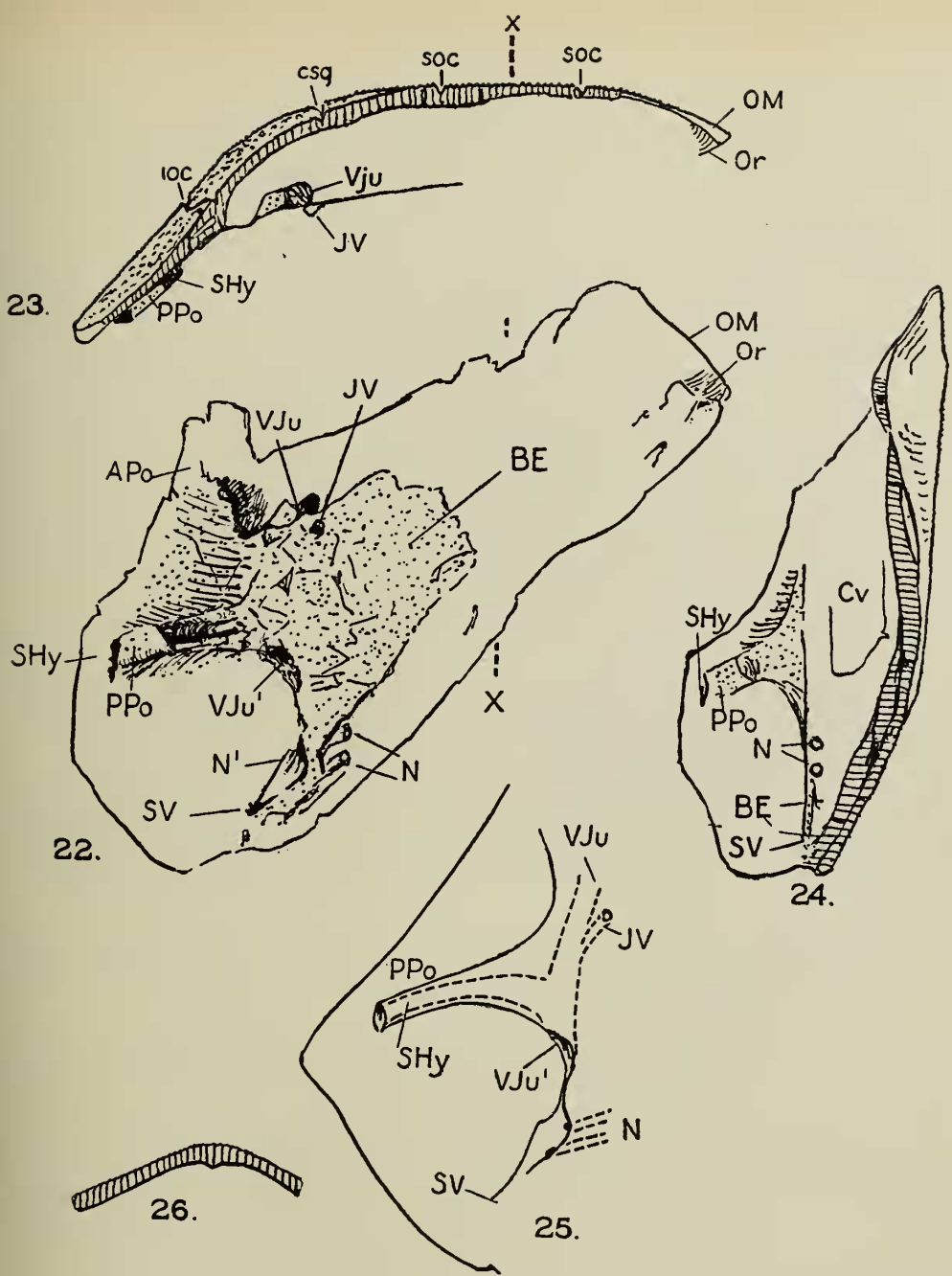
Buchanosteus murrumbidgeensis sp. nov.

TEXT-FIG. 22. Ventral view of holotype, showing part of undersurface of neurocranium. P.27071, nat. size.

TEXT-FIG. 23. Direct front view of same.

TEXT-FIG. 24. Direct left lateral view of same.

TEXT-FIG. 25. Restoration of right posterior corner of undersurface of same, showing passage of vessels in neurocranium.

TEXT-FIG. 26. Cross-section of small median dorsal plate. P.27072, nat. size.

(For explanation of lettering see pp. 303–304.)

unsharklike position, immediately behind the exit of the jugular vein from the anterior postorbital process. Holmgren's objection would clearly be valid if arthrodires were simply selachians, which they are not, whatever their relationships may be (Holmgren, 1942: 161; Stensiö, 1950: 38; Watson, 1950: 42); while the vessel in this form seems too big for his interpretation. In spite of its rather posterior position it may well be that this is the hyoid vein as Stensiö first thought, for his 'posthyoidea lateralis' has no modern counterpart comparable in size that I know.[1] The covered-in jugular is seen in the front view lying immediately on the perichondrial bone of the undersurface and just behind it receives a smaller vein running upwards and backwards from the undersurface. The jugular vein passed out behind in the middle of the embayment between the posterior postorbital and the supravagal processes and formed a short groove or notch on the undersurface along the margin (VJu'), immediately behind which is another groove (N') containing the external openings of the vagus canals which are themselves visible on the inner broken surface (N). The lateral wall of the embayment is not seen except for a short distance below and behind the vagus openings, where it is almost vertical, and may not have been ossified, since the bone of the undersurface appears to end in a clear margin, corresponding to the supravagal ridge in *Kujdanowiaspis*.

Other features on the undersurface, which is much cracked, are vermiculating grooves of small blood-vessels.

The form of the hinder margin can be deduced from the shape of the skull-roof, since the internal articular surfaces must have been on the line of the external cervical joints. The occipital region was therefore extremely short.

The form of the orbitotemporal region may be confidently restored from what is known of the holotype of *B. confertituberculatus* (Hills's '*Coccosteus osseus*'), and here we may note the wide suborbital shelf (SS) and the small median cusp (MC) of the concave anterior margin, presumably developed in connexion with the internasal septum.

The fragment of a median dorsal plate (Pl. 30, fig. 4; Text-fig. 26) seems to belong to this species by reason of the similarity of the ornament, but to a much smaller individual showing an unexpectedly ridged back.

REMARKS. The most marked features of the genus *Buchanosteus*, as we know it, are the large nuchal and paranuchal plates, the short centrals and the, partly at least, ossified ventral surface of the endocranium; while this species is apparently distinguished from the genotype by the longer postorbital margin, the shorter paranuchal margin, and the very brief preopercular groove. The skull-roof is that of a typical brachythoracid, and there can be no doubt that the creature belonged to that group. Hitherto, besides a brief account of the nasal region of *Coccosteus canadensis* (Stensiö, 1942: 21) the only endocranial ossifications described in this group have been the fragmentary ethmoid and otic regions in *Pholidosteus* and the occipital in *Leiosteus* (Stensiö, 1934a), both aberrant Wildungen genera (Gross, 1932). Stensiö (1945: 24), on the basis of Hills's (1936) description, erected the genus *Buchanosteus* for '*Coccosteus osseus*' and referred it to the dolichothoracids (arctolepids) on the

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[1] Professor Stensiö kindly informs me that he now finds that there is no canal piercing this process in *Kujdanowiaspis*, which further emphasizes the difference between the two types of skull.

grounds of the similarity of the postethmoidal bones as then described. The new material shows, however, that although there are similarities, these are no more than one would expect in two groups of arthrodires, and there are important differences,
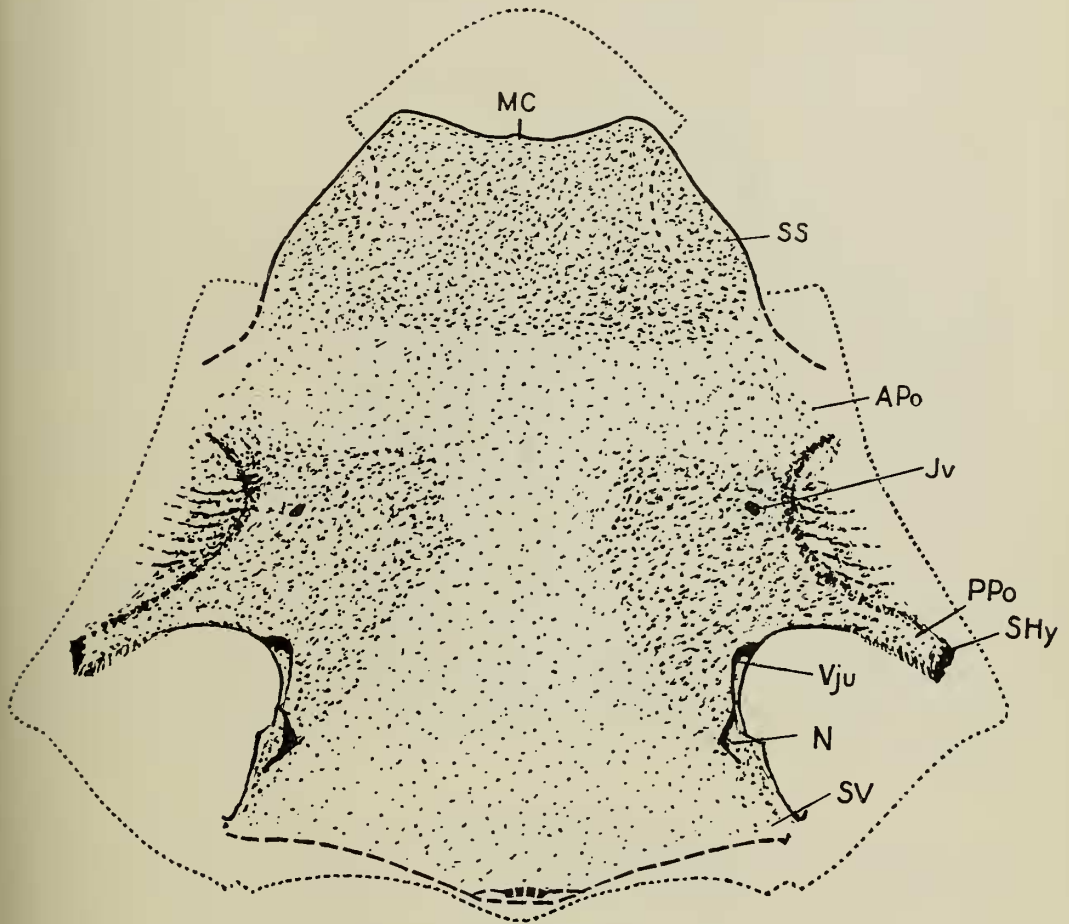
Buchanosteus murrumbidgeensis sp. nov.

TEXT-FIG. 27. Restoration of undersurface of neurocranium flattened out with outline of skull-roof superimposed; orbito-temporal region based on Hills's (1936) specimen. Known areas heavily stippled.

(For explanation of lettering see pp. 303–304.)

among which we may note the larger suborbital shelves, the single posterior postorbital process, the complete enclosure of the jugular vein in the two postorbital processes, the very short occipital region, the entirely different cross-section in the postorbital region and, by no means without significance, the median ethmoid cusp.

It is not altogether easy to reconcile this neurocranium with what has been published of the neurocranium in *Pholidosteus*, the only brachythoracid of which we have an account of comparable parts. The fragmentary otic region of *Pholidosteus* (Stensiö, 1934a; pl. 4, figs. 2–4; text-fig. 7), in spite of its breadth, appears to represent only the anterior postorbital process (of which nothing is known in *Buchanosteus* except the proximal part of its hinder margin), and this requires that the identification of some of the canals be reconsidered. For instance, that labelled *c.hy* is possibly that of the 'vena mandibularis' in *Macropetalichthys*, and not the v. hyoidea, which would have traversed the presumably cartilaginous posterior process, entering at *cx*, while the main jugular canal, instead of leaving the anterior process at *ju*, is entirely enclosed and passes out at *cy*. The ethmoidal region of *Pholidosteus* (Stensiö, 1934a: pl. 11, fig. 5; pl. 12, figs. 1, 2; text-figs. 1–3), is so laterally compressed and modified by the enormous, forwardly-placed orbits that comparison with the imperfectly known dorso-ventrally flattened region of *Buchanosteus* cannot be usefully made. One may doubt whether the differences are other than those due to specialization in different directions, although Stensiö (1942: 21) specifically states that this region in *Coccosteus canadensis* is fundamentally as in *Pholidosteus*.

As for the occipital region, all we know is that in *Buchanosteus* it was extremely wide, even shorter than in *Leiosteus* (Stensiö, 1934a: 37), and much shorter than in the arctolepid *Kujdanowiaspis*.

Family TAEMASOSTEIDAE

DIAGNOSIS. Brachythoracid arthrodires having the paranuchal plate long and leaf-shaped, with all its sides evenly convex and all but the inner posterior angle rounded, overlapped only by the nuchal plate which it exceeds in length.

Central plates narrow behind, marginal plates very long and postmarginal plates large. Ornamentation finely pustulate. Main lateral line groove deeply incised and diagonal in direction, connected at posterior end with extremely short posterior pit-line groove.

Genus *TAEMASOSTEUS* nov.

DIAGNOSIS. As for family (only genus).
GENOTYPE. *T. novaustrocambricus* sp. nov. (only species).

Taemasosteus novaustrocambricus sp. nov.

(PL. 31, FIG. 3; TEXT-FIGS. 28–30)

DIAGNOSIS. As for family and genus (only species).
MATERIAL. Unique holotype, a left paranuchal plate (P.27070).
FORMATION AND LOCALITY. Middle Devonian: Parish of Taemas, Murrumbidgee River, N.S.W.
DESCRIPTION. The specimen was originally attached by the external surface to its matrix, a large piece of hard, grey, marine limestone containing the remains of numerous brachiopods. The matrix was, however, removed with acetic acid and the

whole bone is now beautifully exposed on both surfaces (Text-figs. 28, 29). It is in very fine condition, apparently quite uncrushed, and apart from slight marginal chipping owing to the extreme thinness of the bone there, and the loss of part of the articular process and hinder margin, it is complete. The plate is 9·2 cm. long and a little more than 6·5 cm. in width, so that the fish was a large one. For a paranuchal
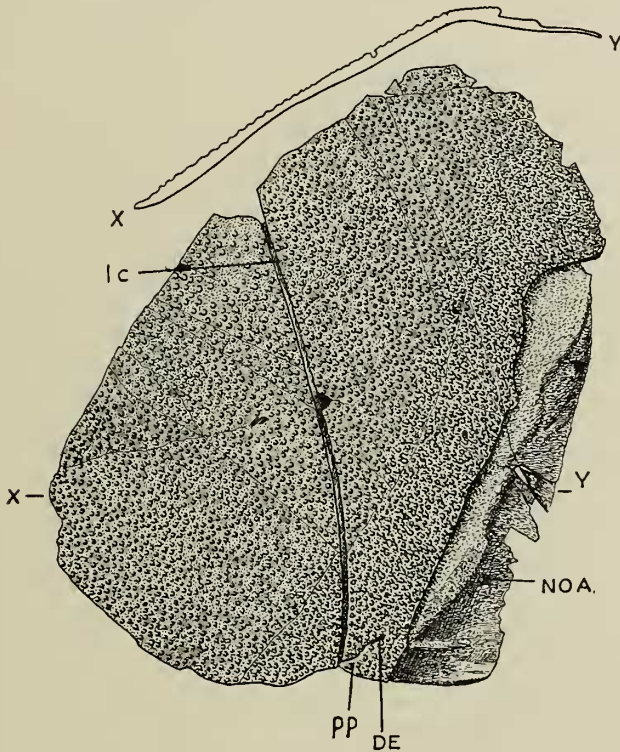
Taemasosteus novaustrocambricus gen. et sp. nov.

TEXT-FIG. 28. Paranuchal plate, with cross-section at X–Y. The holotype, nat. size.
(For explanation of lettering see pp. 303–304.)

the plate is distinguished by the simplicity of its outline, for all the margins are virtually entire, showing a continuous but varying convex curvature, except at the posterior inner corner which is angular, and the notch where the lateral line runs on to the marginal. The plate is gently bowed lengthwise, but is much more strongly convex across the breadth, being roughly divided by a rounded angle of about 25° running directly forwards from the start of the sensory canal into a long, narrow, median surface that formed with the nuchal a horizontal flat crown to the head and a large sloping lateral area.

The whole of the exposed surface is covered with fine tubercles which consist individually of a small shining conical cap decorated with numerous fine radiating

ridges on a very much wider (sometimes three or four times as wide) roughened base passing into numerous irregular roots which cross and anastomose with those of its neighbours, and in between which are the external openings of tubuli (Pl. 31, fig. 3). However, the surface is seldom fresh and usually the fine ridges are worn away and the caps smooth. The upper surface of the overlapped area shows the openings and
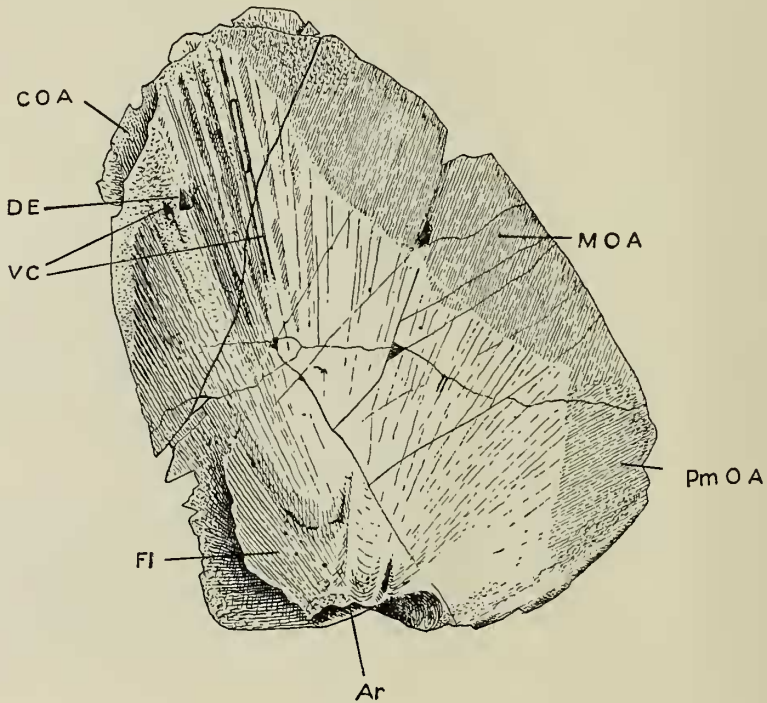
Taemasosteus novaustrocambricus gen. et sp. nov.

Text-fig. 29. Undersurface of holotype.

(For explanation of lettering see pp. 303–304.)

part of the vermiculating tubules of the spongiosa, very much as if it were a cut surface. The exposed surface is crossed by the deeply incised main lateral line groove which runs forward from the articulation near the nuchal overlap and quickly curves outwards to run diagonally to the outer margin at about two-thirds of the way along its length. At its hinder end it gives off a very short, curved, and much shallower branch, the posterior pit-line groove, ending in a longish pit. This pit was the dorsal aperture of the ductus endolymphaticus which ran forwards through the bone underneath the margin of the nuchal overlap, forming a short, increasingly conspicuous ridge on the anterior part of the undersurface. The lower, anterior aperture is not preserved, but it cannot have been far from where the canal now ends (DE, Text-fig. 29).

The area overlapped by the nuchal plate is remarkable for it shows that the nuchal was very much shorter than the paranuchal. This area is flat in front but curves down mesially behind where it is divided into two by a longitudinal step, which deepens and then curves into the ornamented lateral margin near the hinder border of the plate. Here also the lower part of the area rises owing to a thickening of the bones for the formation of the articular socket. This part of the plate is much the thickest and the undersurface shows that here was the centre of ossification, as indicated by the radial structure of the bone. The radial structure is indeed remarkably
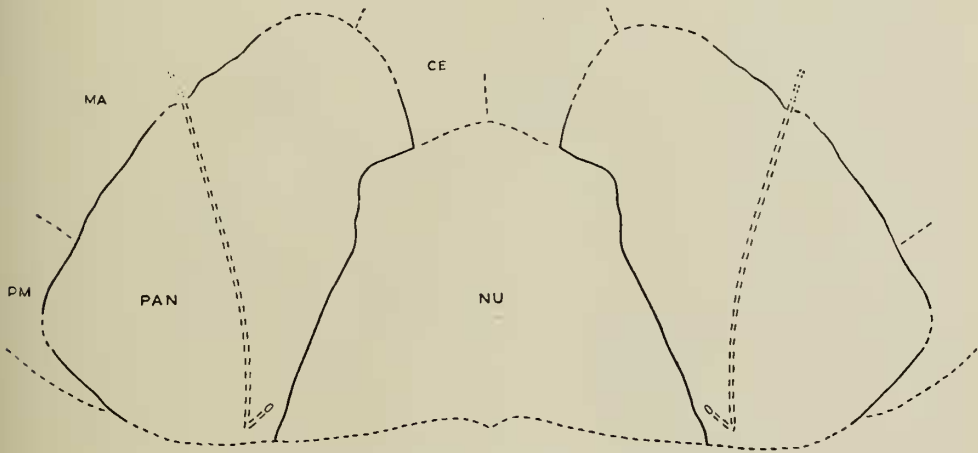
Taemasosteus novaustrocambricus gen. et sp. nov.

TEXT-FIG. 30. Restoration of posterior half of skull, flattened out. × $\frac{2}{3}$ approx.
(For explanation of lettering see pp. 303–304.)

clearly shown, with one or two of the vascular canals of unusual size, particularly one running close to the foramen of the ductus endolymphaticus on its mesial side and another on the other side of it rather farther away (VC, Text-fig. 29).

However, the most conspicuous feature on the lower side of the plate, which of course is concave, is a thin, deep lamina of bone (Fl) that forms part of the support of the articular socket, which is itself missing. The lamina lies at a low angle, about 10°, directed towards the nuchal margin with which its base is roughly parallel, although its extent towards the centre of the head is uncertain. That the articular parts were massive is indicated by the wide, rounded ridge which runs from the hinge outwards along the posterior margin, flattening as it goes.

Along the thin, outer margin there are wide areas devoid of the basal layer showing the degree of overlap on to the marginal plate (MOA) and the postmarginal plate (PmOA). The former is extremely long, equal to nearly three-quarters the length of the plate and $2\frac{1}{2}$ times the postmarginal overlap, which it meets at nearly a right angle. On the other hand, the area of overlap on to the central plate in front is short and if the nuchal plate is properly orientated, the central plates must have been unusually narrow (Text-fig. 30).

The microstructure of the bone is interesting. The spongiosa forms almost the whole of the bone, for the basal laminated layer is exceedingly thin and usually rubbed away, while the surface layer seems confined to the caps of the tubercles.

The spongiosa varies in texture from place to place. Near the articulation, the broken surfaces show the bones to be almost solid with fine tubules, and at the articulation itself it is vertically laminated. Away from this point the thick margins at each end of the overlapped area are very spongy, but the thin margin in between shows distinct division into two or three laminae. As in many arthrodires a marked feature of the bone is the radial arrangement and straightness of many of the canaliculi in the lowest part of the spongiosa. The presence of these canals (Heintz's 'ossification rays', 1932: 122, 172, &c.) on the undersurface of the bone has already been noted and they are particularly clear where the basal layer on the surface is slightly damaged; but even where this is present the canals pierce this surface to form open pores of various sizes, and are particularly numerous near the hinge or centre of ossification. The great majority of these vascular canals are very fine, as fine as the vermiculating canals with which they are associated, but they seem to grade up into much larger canals (VC) of which the largest, measuring nearly 2 mm. in diameter, has been identified with the ductus endolymphaticus.

REMARKS. Although the exact orientation of this paranuchal plate cannot be determined with complete accuracy owing to the absence of the hinge area, we may make a reasonable attempt at restoring part of the back of the skull (Text-fig. 30), which seems to have had several unusual features. The large size of the paranuchals relative to the nuchal plate is, so far as I know, unique, as is also its rounded shape.

The marginal plate must have been unusually large, and recalls in this respect certain of the Wildungen genera, such as *Rhinosteus* and *Leptosteus* (Gross, 1932: text-figs. 7, 12), and further resembles them in the extent and position of the postmarginal plate. The presumed narrowness of the posterior end of the central plates is also seen in *Leptosteus* which is a much laterally compressed form, whereas *Taemasosteus* certainly is not; but these resemblances are interesting probably only as showing that this form comes within the known limits of generic variation in the brachythoracid arthrodires, and not as indicating closer affinity to any particular form or forms.

BRACHYTHORACIDI *incertae sedis*

(TEXT-FIGS. 31–35)

MATERIAL. An isolated left posterior superognathal (P.27074).

FORMATION AND LOCALITY. Middle Devonian: Barber's, Goodradigbee River, N.S.W.

DESCRIPTION. As received, only a small part of this specimen was exposed, but it has now been completely disengaged from its matrix by means of acetic acid. The length is only 9·2 mm. Seen from above (Text-fig. 33) the bone has in front a strong mesial process. The hinder margin of this process is at right angles to the body and the anterior runs forwards and inwards at about 45°. Most of the anterior outer face is missing, but behind the break the outer margin continues backwards in a gently sinuous curve to meet the inner side in a point.

The anterior face of the mesial process is that in contact with the anterior superognathal (cf. Heintz, 1932: 148, text-figs. 28, 29). It is roughly triangular, narrowing and sloping gently inwards and downwards to the origin of the blade. The broad upper part is more or less flat, but a groove develops below along the front edge, which is straight but somewhat sloping.
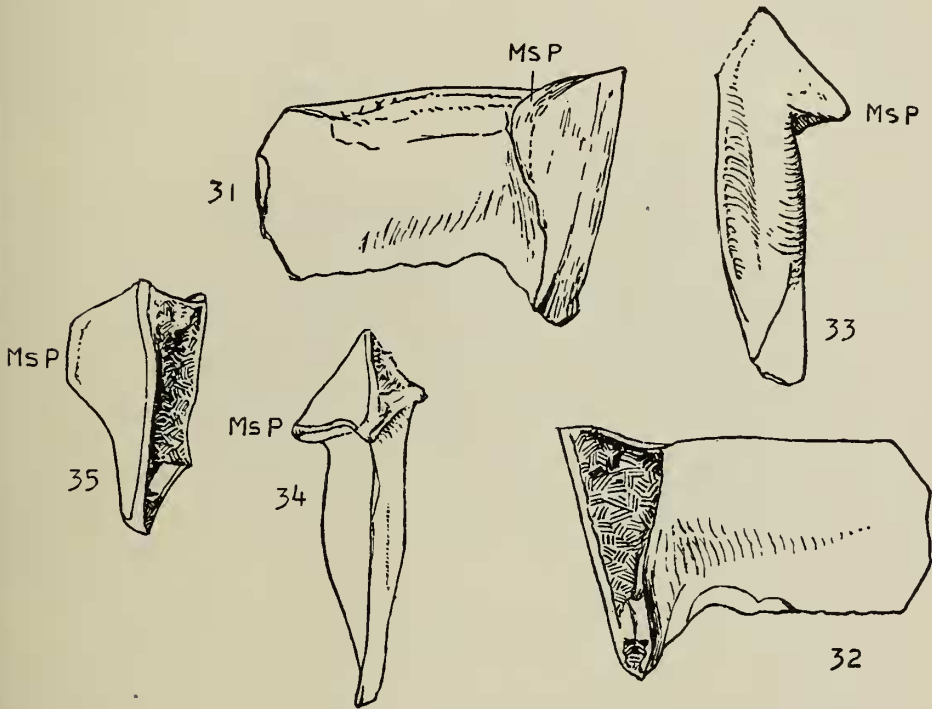
TEXT-FIG. 31. Left posterior superognathal of undetermined brachythoracid, inner view. P.27074, ×5.

TEXT-FIG. 32. The same, outer view.

TEXT-FIG. 33. Palatal (dorsal) surface.

TEXT-FIG. 34. Direct oral (ventral) view.

TEXT-FIG. 35. Front view.

(For explanation of lettering see pp. 303–304.)

The corresponding face on the outer side has decayed (Text-figs. 32, 35) except for a narrow vertical selvage along the front margin and a fragment below. The form of this face is uncertain, but the anterior selvage is transverse to the length of the bone and suggests that the upper part was rounded, although the fragment below shows a vertical division into two facets. The whole face is separated behind from the body of the plate by a low, nearly vertical ridge which runs to meet the median and mesial ridges in a point at the start of the blade.

The blade is single and in side view (Text-figs. 31, 32) is irregularly concave, running upwards and backwards in a wavy line and then curving round 45° to continue backwards to the hinder end. From below (Text-fig. 34) the blade is almost straight with a gentle inward curve towards the rear. The only shearing surface is in the form of two crescentic areas at the angle and on the outside (Text-fig. 32).

The posterior end is almost as thin as the blade and was apparently rounded without denticles.

The upper surface, by which it was attached to the palatoquadrate, shows a distinct longitudinal groove near the outer margin, which is raised and sharp, and there is a slight eminence over the mesial process but nothing so pronounced as that in *Dinichthys* (Heintz, 1932: text-fig. 28).

The break in the outer face shows, rather surprisingly, that this part of the tooth was hollow, or at any rate of very loose structure, with a distinct inner longitudinal wall under the groove on the attached surface.

REMARKS. This small, probably juvenile, plate shows sufficient resemblance to the corresponding plates of *Dinichthys* (Heintz, 1932: text-figs. 28, 29) to make its identification as a posterior superognathal clear, but it is very different in such detail as the form of the mesial process, the irregularity of the blade, and the external shearing-surface, &c. The plate is of about the same size as Watson's (1934: 440, text-fig. 1c) gnathal of 'a nearly full grown but not old specimen' of *Coccosteus decipiens*, but differs from all the figured plates of that and other species of *Coccosteus* (Gross, 1933c: pl. 2, figs. 12, 19; text-fig. 10; Heintz, 1938a: text-fig. 3) in the stronger but lower mesial process, in the absence of posterior and external denticles, and in the irregular form of the single blade. Indeed, it differs considerably from all the known posterior superognathals (cf. Heintz, 1931c: 247, text-fig. 4; Dunkle & Bungart, 1946: text-fig. 3; Dunkle, 1947: text-fig. 2A).

Finally, it is interesting to note that in *Pholidosteus* (Stensiö, 1934a: 25, 36, pl. 11, fig. 5, pl. 12, figs. 1, 2, text-figs. 3, 12) the impressions on the mesial face of the palatoquadrate together ($p+gr. psg$) correspond very well with the form of the attached surface of the new plate, p being the impression of the mesial process; but if this is correct, then obviously the palatoquadrate will not be as vertical in position as it was described.

This plate is almost certainly that of a brachythoracid, although the only other arthrodire material found at Barber's was the arctolepid *Williamsaspis*. It is clearly too small, even though juvenile, to have belonged to *Taemasosteus*, but could have been carried by *Buchanosteus*. That, however, is just conjectural and it may represent yet another arthrodire genus.

III. THE GENUS *NOTOPETALICHTHYS* A. S. WOODWARD, 1941

Notopetalichthys hillsi A. S. Woodward

(TEXT-FIGS. 36, 37)

Recently I have had the opportunity of re-examining the unique specimen described by Woodward (1941) and am now able to add some details to the original description. The median length over the curve is exactly 10 cm. as preserved, but

it is clear that the hinder margin of the centronuchal plate is not complete, as Woodward states, and doubtless continued farther backwards as in other petalichthyids (Stensiö, 1948: text-fig. 72). On the other hand, the whole rostral plate is now uncovered and projects forwards considerably (Text-fig. 36). The skull is distorted, being pushed diagonally towards the left anterior corner, but nevertheless, the original shape can easily be made out. The orbits and with them the whole central part of the head are raised rather abruptly, so that the marginal area forms a flattened brim, especially in front, but the skull is otherwise flat longitudinally.
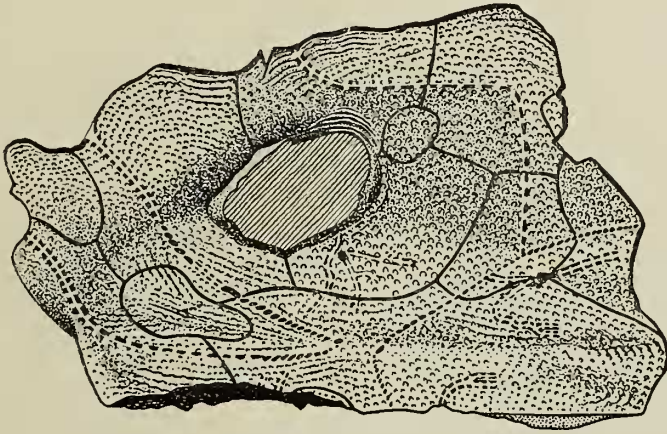
Notopetalichthys hillsi A. S. Woodward.

TEXT-FIG. 36. The holotype showing outlines of plates and sensory grooves. Nat. size.

The main sensory canal system is normal for the group, being like that in *Epipetalichthys*, without connexion between the supraorbital pair and the transverse posterior pit-line. It consists of series of well-defined pits, or grooves, merging into continuous canals marginally. In addition, on the lateral central, behind the eye and spilling on to the centronuchal plate are two sets of shallow pit-line grooves: a slightly curved transverse groove that may be the remnant of the central sensory groove eliminated by the inward migration of the eye, and an irregularly ramifying series immediately behind representing the median pit-line. Still farther behind, coming off inwards and backwards from the posterior pit-line canal is another short irregular groove passing very close to the opening of the ductus endolymphaticus and bifurcating distally; while from the opening itself, which is just inside the margin of the anterior paranuchal plate, a short groove runs straight backwards and slightly outwards on the posterior paranuchal.

The outlines of the component bones are now clearly to be distinguished and form a very characteristic pattern. The jutting rostral is separated for a considerable distance by the preorbital plates from the rather elongated pineal plate, which bears

a central macula. The bent, diagonally disposed, lateral central plate (CL, Text-fig. 37), with ramifying sensory grooves, occupies nearly half of the margin of each very large orbit. Just behind the orbit, at the junction of the lateral central, postorbital,
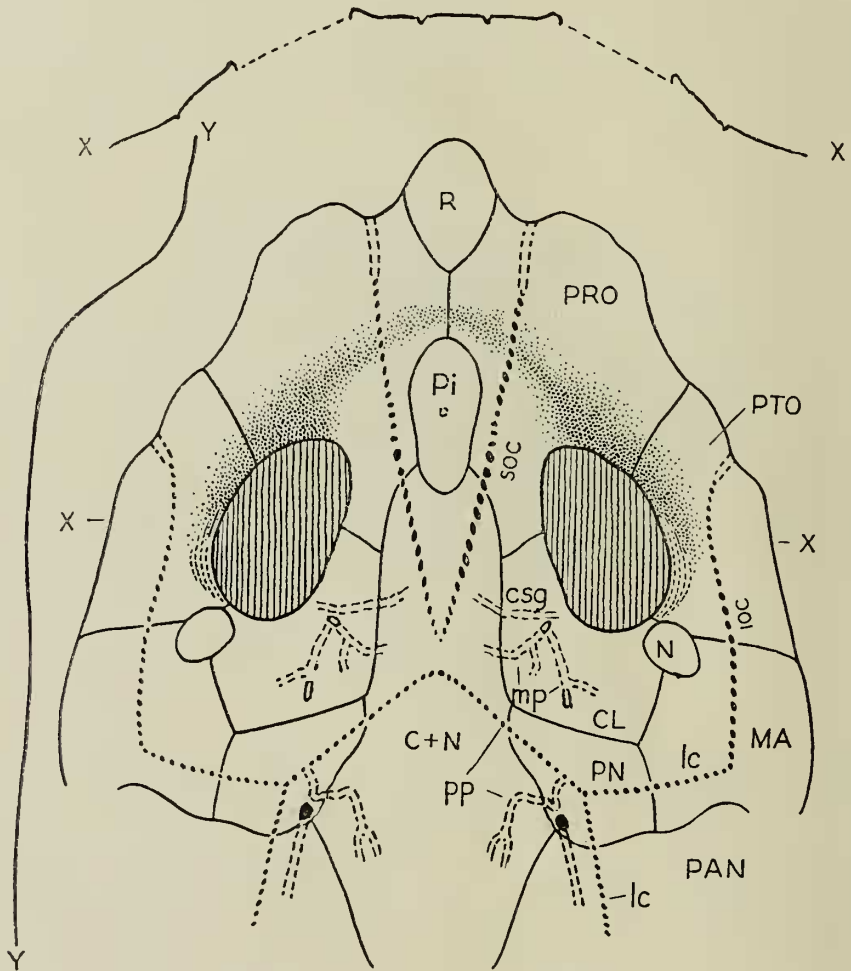
Notopetalichthys hillsi A. S. Woodward.

TEXT-FIG. 37. Restoration of skull-roof. *X–X*, transverse and *Y–Y* median longitudinal profiles.
(For explanation of lettering see pp. 303–304.)

and margin plates, is a small ovoid plate, but whether this is a diagnostic character of the species present on both sides or an odd individual malformation cannot be determined, since the left side is not preserved.

An attempted restoration of the specimen is given in Text-fig. 37.

The genus is a well-marked one and may be briefly diagnosed as follows: a petalich-thyid with marginal area of head depressed, especially in front of eyes, forming well-marked brim: orbits very large, somewhat oblique, placed on sides of slope from main raised area. Rostral plate small, projecting forwards and completely separated by the preorbital plates from the rather elongated pineal plate which indents the centro-nuchal. Lateral central plates oblique and somewhat L-shaped, forming large part of orbital margin. Small oval plate at junction of lateral central, postorbital, and marginal plates. Sensory canal systems in form of lines of deep pits in shallow grooves: supraoccipital canals not meeting posterior pit-line canal. Central sensory groove and median pit-line groove represented by short, shallow grooves, mainly on lateral central plates, the former simple and curved, the latter branched: similar grooves running irregularly from main posterior pit-line canal backwards and in-wards past external opening of the endolymphatic duct.

GENOTYPE. The unique species, *N. hillsi* A. S. Woodward.

FORMATION AND LOCALITY. Middle Devonian: Goodra Vale, N.S.W

IV. PECTORAL FINS OF ARTHRODIRES

Direct evidence of pectoral fins is given by a number of arthrodires and their relations. Parts of the fin itself have been figured in an undetermined genus and in *Dinichthys* (Heintz, 1932: 197–8, text-figs. 85, 86, 90), *Coccosteus* (Heintz, 1938a: 20, text-fig. 5), *Rhachiosteus* (Gross, 1938a: 199, pl. ii, fig. 2; text-figs. 1, 5a), which are all Brachythoraci, in *Gemündina* and *Stensiöella* (Broili, 1933a: pls. ii, iii, text-figs. 3, 8), and *Pseudopetalichthys* (Broili, 1933b: 426, plate, fig. 1; text-figs. 3, 5; Stensiö, 1944: text-fig. 18); while the articular surface of the scapulo-coracoid is known in the brachythoracid *Enseosteus*, the arctolepid *Kujdanowiaspis*, the related *Palaeacanthaspis* (Stensiö, 1944), and in *Williamsaspis*. The pectoral fins were apparently long-based in all the brachythoracid examples, in *Coccosteus*, *Rhachiosteus*, Heintz's unknown genus, and *Enseosteus*; but were short-based in the arcto-lepids, in both *Kujdanowiaspis*, with its full body-armour, and in *Palaeacanthaspis* in which the body-armour is reduced. This clearly shows that the length of the fin-base is not to be correlated with that of the body-armour, and suggests that in arthrodires it had become a systematic rather than a functional character. The pectoral fins of *Williamsaspis*, although small proximally, are in fact long-based to the extent of being borne by a horizontal linear series of about nine separate basals on an elongated, slightly raised, articular ridge, reminiscent of the restored scapulo-coracoid of *Enseosteus* (Stensiö, 1944: text-fig. 14) but on a smaller scale. Thus *Williamsaspis* still has obvious traces of a type of fin, long-based, lost in the more specialized arctolepids, but largely preserved by the brachythoracids. Stensiö (1944: 16) considers that the long-based type of the brachythoracids is the more primitive, which seems reasonable enough, but if the brachythoracids are primitive in their pectoral fins, they are certainly specialized in their body-armour to the extent that it is shortened laterally (Heintz, 1931b: text-fig. 10). The brachythoracids retained long-based pectorals but reduced their armour, while the arctolepids generally increased their armour to the extent of producing enormous pectoral spines,

and reduced the pectoral fin-bases, so that the common ancestor of both groups must therefore have had full body-armour like the arctolepids but with a long-based pectoral fin like that of the brachythoracids in place of the spine. Heintz (1938a: 23, text-figs. 6, 7) has made an interesting morphological series of arthrodire reconstructions in which the long-spined forms precede the short-spined brachythoracids. In this series Heintz (1938a: text-fig. 6) gives 'Jaekelaspis' a narrow fringe in the pectoral bay—'a slightly developed skin-fold'—which demands a slit behind in the spine and a space between the anterior lateral and anterior ventrolateral plates. Since such remnants could have had little functional value, Heintz was presumably anxious to retain in these forms some element of the fin in order to avoid the apparent 're-creation' in the adult of pectoral fins in the brachythoracids after the complete suppression of the lateral fin-folds in the arctolepids. But such a device could hardly have served such a purpose. A fin so specialized in respect of the spine and degenerate in respect of the web as that shown in Heintz's restoration of 'Jaekelaspis' is certainly not going to develop later into a serviceable pectoral fin such as the brachythoracid arthrodires must have had, even if it was relatively stiff and acted largely as a gliding plane, capable only of slight movement as a whole or by undulation. It is true that we do not know the form of the very early stages of arthrodires which, like most juvenile ostracoderms, seem to have been unarmoured. Even if juveniles had retained pectoral fins eliminated in the adult, there is no evidence to show that the adult could have regained a character so lost, although Watson (1934: 448) has suggested the agency of a latent limb-bud for regaining a pectoral fin completely lost in ancestral forms. But what is more to the point, the arctolepids with long pectoral spines, such as 'Jaekelaspis', are clearly the overspecialized end-terms of a series that could not have given rise to the progressive brachythoracids or to anything else, and their fate was the fate of all such series, extinction. Westoll (1945a: 350; 1945b: 383, text-fig. 3) has much elaborated Heintz's ideas on the development of arthrodire pectoral fins, grafting on to them his 'bone-jacketing' theory and providing the animals with a heterocercal tail. He supposed that the spines were extensions of the body-wall completely covered with dermal bone without even the fringe of fin postulated by Heintz, and that subsequently part of this pectoral body-extension was freed to form fin-membranes, while the prespinal lamella was considered to be possibly 'an integral part of the necessary structural bracing of such hydrofoils, the necessity for which disappeared with the differentiation of a controllable fin-membrane'. However, this 'fin-fold: jacketing: fin-release' sequence seems clearly to be disproved, at least in relation to the development of the arthrodire pectoral fin, by Stensiö's (1944) demonstration that the 'prespinal lamella' was the perichondrial ossification of the mesial surface of the scapulo-coracoid cartilage, and that the pectoral fin-spine was borne by a lateral process of the cartilage related to the backward concentration of the originally extensive fin-base. It would appear, therefore, that the spine and the cartilaginous process were developments subsequent, and not prior, to the formation of the pectoral fin; and further, that the spine, instead of being the 'ossified dermal jacket of the entire pectoral appendage', covered only the process of the girdle, and that the fin in at least some cases, such as Kujdanowiaspis and Williamsaspis (to name both a long- and short-spined form), occurred in a developed and

concentrated form behind it. Indeed, it is difficult to believe that any of the arcto-lepids were without effectively controllable pectoral fins, as Heintz (1938a: 23) tentatively and Westoll (1945b: 384) more definitely suggest. Assuming, of course, that there were no unknown hydrostatic organs, they would seem thus to have been dynamically incompetent, especially so if they had heterocercal tails, as seems possible. They present a similar sort of problem to that of *Pteraspis* before the caudal region was known, but with different factors. In *Pteraspis* it was possible to predict (White, 1935: 382) the hypocercal tail on the ground that that was the only form which would give an upward and forward thrust to the head (see Grove & Newell, 1936: 289) to counterbalance the depressing effect of the weight of an armoured forebody in a fish-like creature without pectoral fins—otherwise, in fact, *Pteraspis* could never have got off the bottom, for 'the buoyancy and the upward thrust due to the entrance of the rostrum' (Westoll, 1945a: 353; Kermack, 1943: 23–27), let alone of the undersurface, would be inoperative once it was grounded on a muddy floor, especially if it rested, as Westoll suggested, 'with the snout somewhat de-pressed': an even-lobed tail would then as often as not have pushed the snout into the mud, and a heterocercal tail certainly would have done so. The 'typical' arcto-lepids (that is dolichothoracids) were similarly burdened with a heavily plated fore-body as opposed to a lightly protected caudal region, but with the important differ-ences that they had very large pectoral spines, a flat undersurface, and a movable head, and they did not have a hypocercal tail. Doubtless the spines and the under-surface were valuable as gliding-planes when the fish was in motion, but clearly they would be useless in the take-off, especially from soft ground, unless there were means of raising the fore-part, particularly as the pectoral spines sloped forwards and downwards (Heintz, 1935: 238), the effect of which would in itself be to depress the anterior end until that part were raised sufficiently to make the spines horizontal. This raising could be achieved either by the thrust of the tail alone, if hypocercal, as in *Pteraspis*, or by use of an anterior plane inclined upwards, if the tail were even-lobed or heterocercal. Unfortunately there is no direct evidence of the condition of the tail fin in arthrodires except in the brachythoracid *Coccosteus*, in which it is supposed by Heintz (1935a: 15, 19, text-fig. 4 (4)) to have been possibly heterocercal —a supposition which is clearly supported by specimens in the British Museum collections, Nos. P.180, P.10798, and especially P.187. This form is adopted for both brachythoracids and arctolepids by Westoll (1945b: 384, text-fig. 3). In the absence of evidence to the contrary this premiss as to the tail-form in arctolepids must be accepted for the time being, and it follows that there must have been means of countering the initially depressing effects of both the heterocercal tail and the downward slope of the fin-spines, and since the body lay flat on the bottom when resting, the anterior rising plane must have been provided either by the undersurface of the movable head or by pectoral fins. Westoll (1945b: 384–5), although he does not specifically deal with the problem of the take-off, denies the existence of fins in arctolepids, as already noted, and seems to rely on the movement of the head allowed by the cervical joints for 'inducing and controlling pitching'. The up-and-down movement of the head would doubtless be of prime importance in altering elevation in the vertical plane when the fish was water-borne, very much as the dog-fish with

amputated pectorals uses the undersurface of its head (Harris, 1936: 491). The tendency of the downwardly inclined pectoral fin-spines and heterocercal tail to put the swimming fish into an uncontrollable, increasingly steep dive could also have been countered by this head movement. Whether the arctolepid with its heavy fore-end and inflexible back could have got off a soft river- or lake-bed by the same device alone seems unlikely, and in spite of the absence of direct evidence as to their presence it would appear to be clear that controllable pectorals were in fact developed.

This view received support in a recent reconstruction of *Phlyctaenaspis* by Denison (1950: 578, pl. iii, fig. 2) based on the form of the plates. Even more convincing is the form of the hinder part of the scapulo-coracoid in various members of the group, including the extreme *Arctolepis* (*Jaekelaspis*) itself, as shown by the 'prespinal lamella' (e.g. Heintz, 1929: pl. vii, pl. xv, fig. 2; 1937: text-figs. 3 C, D), which in outline is similar to that in *Kujdanowiaspis* (Stensiö, 1944: text-fig. 17 B), showing a considerable posterior face along the pectoral embayment. On this evidence pectoral fins may likewise be expected in the arctolepids, although on account of the peculiarities of *Kujdanowiaspis* in the matter of the lost hinge-joint, not necessarily of the same quality. That pectoral fins were standard equipment for the brachythoracids is clear enough from the examples known, and it is most unlikely that the aberrant members of the group, such as *Brachydirus* and the thin Wildungen genera, like *Oxyosteus*, should have discarded such advantageous features. However, owing to the form of the armour the fins must, as Westoll (1945*b*: 385) suggests, have moved backwards, not necessarily on to the flank, but to the level of the AL–AVL suture, where they would have been no more posterior in position relatively than in *Williamsaspis*. The girdle-bearing function of the spinal plate would then be taken over by the two plates mentioned, which in *Williamsaspis* already share it. It would seem even more necessary for *Synauchenia* (Gross, 1932: 45) to have had pectoral fins since the head was completely immobile on the body.

The remarks concerning the necessity for pectoral fins obviously apply to other groups of similar general form, such as the petalichthyids, in spite of the supposed absence of the 'prespinal lamella', which is not necessarily very important, as it might well be that the scapulo-coracoid lacked the perichondrial bone-layer. The presence of pectoral fins would seem to make the derivation of *Gemündina* from *Lunaspis* a little less unlikely (Westoll, 1945*b*: text-fig. 5), but in any case the suggestion that *Pseudopetalichthys* was an intermediate form is most doubtful, for not only is there good reason to suppose that in that genus the whole of the supposed AVL is not the scapulo-coracoid, as Broili first suggested, but its shape in Westoll's figure is wrong, with the fin misplaced and too wide. A fish having such a specialized fin as *Pseudopetalichthys*, with its articular area concentrated to bear only three stout backwardly directed radials, would be a most unlikely lead to the skate-like *Gemündina*.

Finally, before leaving the subject of pectoral fins, it is perhaps worth while to comment on Westoll's (1945*b*: 391, text-fig. 7) suggested derivation of the antiarchan arthropterygian fin from the arctolepid fin-spine. Quite apart from Stensiö's (1944) demonstration of the form of the arctolepid pectoral spine and endoskeletal girdle, the idea that a firmly fixed spine should become loose, acquire a complicated articu-

lation at the base and another half-way along, and break up into a complex series of plates seems to go beyond the widest bounds of probability; in any case, one highly specialized character is not likely to turn into another that is incongruous and equally specialized.

V. THE FORMATION OF THE ARMOUR

Stensiö (1945: 5–6) has given an order of formation of the armour in arthrodires relative to the appearance of the cervical joints. These he considers 'cannot possibly have existed in the ancestors of the arthrodire group, but must be assumed to have arisen very early in the arthrodire group itself'. The force of this statement obviously depends on one's definition of the 'arthrodire group'—and of 'ancestors'. Stensiö suggests that the formation of the exoskeleton of the head and shoulder-girdle—that is, apparently the whole of the body-armour less the median and spinal plates (Stensiö, 1944: 15, 50, 79; 1945: 6)—was accomplished in the primitive gnathostome form from which the arthrodire group was derived before the articulation was formed, and that 'each half of the exoskeletal shoulder was in all probability rigidly attached dorsally (i.e. by the anterior dorsolateral) to the skull-roof'. Subsequently, 'When in early arthrodires the head began to be moveable against the trunk, two halves of the exoskeletal shoulder-girdle were loosened from the dermal skull-roof. In need of a new rigid attachment dorsally they became intimately connected with the scales situated between their dorsal ends, owing to which these scales lost their mobility and fused together into two large median dorsal plates, the anterior median dorsal plate, and the posterior median dorsal plate, which formed the dorsal wall of the exoskeletal shoulder-girdle.'

The formation of a movable joint behind a head which was rigidly attached to the body would in itself require a rather complicated series of nicely synchronized adjustments. In such a case the loosening of the head from the shoulder-girdle must surely have taken place *pari passu* with the development of the internal articulation and the modification of the musculature, if not before, since some degree of movement would appear to be a prerequisite of its formation. Moreover, so as to allow such movement without damage, there must also have been at least a partial development of the exoskeletal articulation.

However, this development becomes still further involved by the supposition that to meet the loss of rigidity caused by the loosening of the head from the shoulder-girdle, the dorsal scales fused together to form two large median dorsal plates.

The formation at this stage of the exoskeletal articulation would be interesting because it might indicate the point at which the euarthrodires and the antiarchs separated, for the articulations are reversed in the two groups, the trochleae being on the body-armour and the fossae on the head-shield in the euarthrodires, and vice versa in the antiarchs.

As an alternative to this complex sequence of events, we may suppose that the internal shoulder-girdle, the scapulo-coracoid, was primarily horizontal, supporting the primitive horizontal pectoral fin formed from the lateral fin-fold, and that it remained so in the arthrodires, the scapular process being a subsequent development related to the concentration of the radials and the formation of a controllable

pectoral fin. The original exoskeletal support of the shoulder-girdle was therefore formed by the interlateral and possibly the spinal plates, and the attachment to the anterior laterals, apart from a possible marginal selvage (which may have also occurred along the top of the anterior ventrolaterals), followed later with the development of the scapular process.

Again, in the suggested sequence of development of the cervical joints and armour noted above, it would seem possible that the internal articulation was developed before the formation of the plate-armour (and with it the external articulation), and that the ancestors of the arthrodires proper and the antiarchs separated at some point between these two developments, i.e. after the formation of the internal articulation and before that of the armour and external articulation. The latter was surely developed in all lines, and its absence, as in some arctolepids (e.g. *Kujdanowiaspis*, *Euryaspis*), the petalichthyids, &c., is a secondary feature. Westoll (1945*b*: 385) has suggested that the cervical articulation was 'initially a functional adaptation'—it only allowed 'relative movement about a transverse axis, and it would therefore have prevented lateral movements which might induce uncontrollable yawing movements. The up-and-down movement of the head may have been of positive value in inducing and controlling pitching.' It is difficult to believe that yawing (i.e. deviation in the horizontal plane from the intended route) was of much significance in the lives of the early arthrodires, bottom-haunting and poor swimmers that they must have been, or even if it were, that inability to turn the head sideways would have checked it. On the contrary, in view of the importance of lateral head-movements in changing direction (Gray, 1933), the fixity of the head and body in the vertical plane might well have been disadvantageous in correcting involuntary lateral movements. The second suggestion that the articulated head was a means of altering level while swimming seems much more likely and would have been of especial advantage to the ancestral arthrodires before the pectoral fins became more controllable by concentration, particularly if they had heterocercal tails. However, it is possible that this was originally connected with breathing, the movement of the head facilitating this function by a kind of bellows-action. Indeed, if the gill-opening was placed where Stensiö (1944: text-fig. 14) has pictured it—and it could hardly have been very differently placed, unless perhaps a little lower down—movement of the head was apparently essential in some form to allow the slit to open. Moreover, there may, too, have been some connexion between the position of the gill-slit and the neck-construction as shown by the apron described below (p. 292), since the 'pocket' so formed would allow the opening to come farther in and behind the head, where it could open more widely with a smaller movement of the head (Text-fig. 38). If there was a relation between the movements of the head and breathing it is difficult to understand why the articulation ever disappeared, as it undoubtedly did, and what is more, quite early in the history of the group: it had already gone except for overlapping flanges in the Lower Old Red arctolepids *Euryaspis* (Bryant, 1934: 137) and *Kujdanowiaspis* (Stensiö, 1944: text-fig. 17*A*); while the movement of the head must have very nearly ceased, among the brachythoracids, with the development of the extrascapular plates in the Middle Old Red *Coccosteus minor* (Heintz, 1938*a*: text-fig. 2 (1); Stensiö, 1945: text-fig. 12 A; shown also in *C. decipiens* by Gross, 1940:
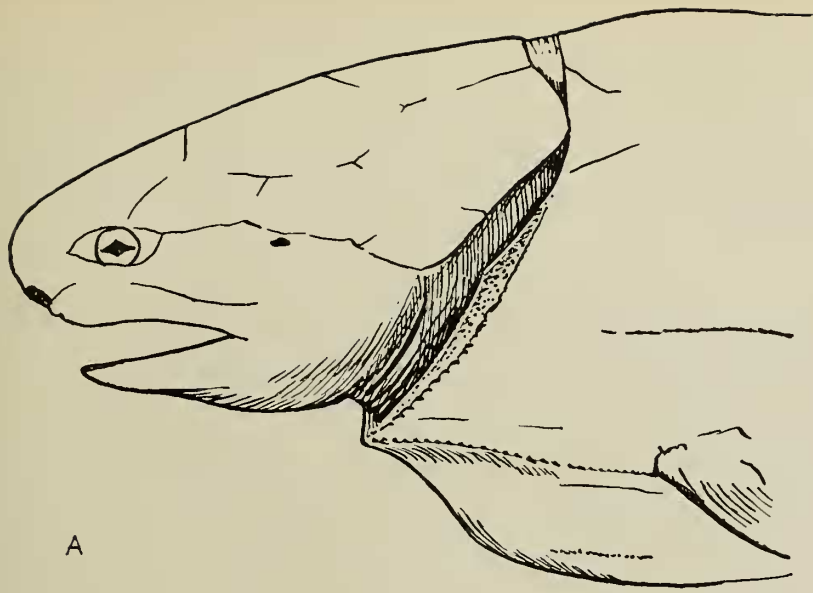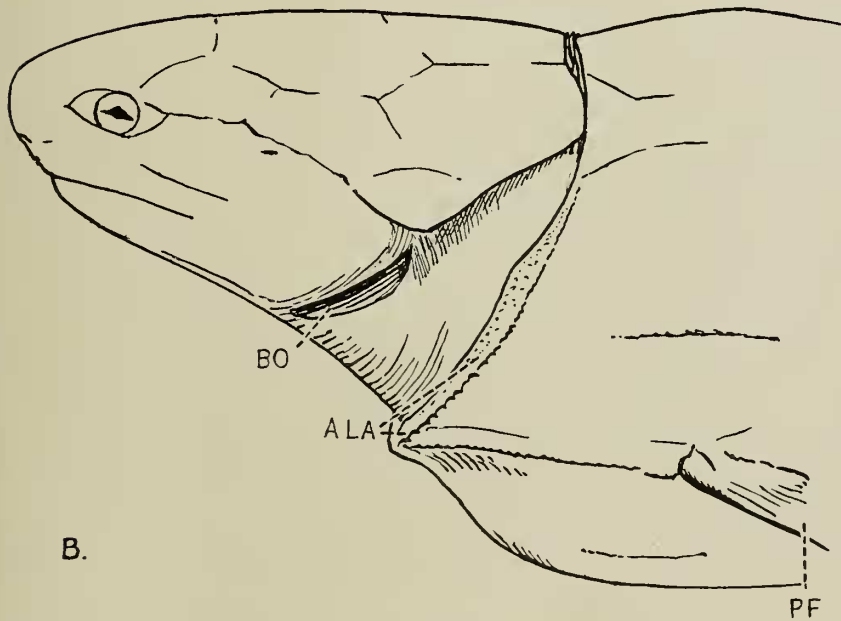
TEXT-FIG. 38. Reconstruction of the head and shoulders of an arctolepid arthrodire (*William-saspis*), showing the supposed constriction of the neck and movement of the head in breathing. A. Inhalant position. B. Exhalant position. (For explanation of lettering see pp. 303–304.)

text-fig. 14c), and completely in the fused head and body-armour of the Upper Devonian *Synauchenia* (Gross, 1932: text-fig. 25).

It is conceivable that in these cases the gill-slit moved downwards into a more chimaeroid-like position where it would open directly below without the need of head-movement—or at any rate into a sort of vestibule formed from the remnant of the neck-pocket.

VI. THE APRON

Structures similar to the apron of the anterior lateral plate in *Williamsaspis* have been described in a number of arthrodires in differing degrees of development and with varying composition (Text-fig. 19). What Heintz considers the 'original' condition (1929: text-figs. 8, 9, 11, 13, &c.; 1934a: 137) is shown by such Lower Devonian arctolepids as '*Jaekelaspis*' in which the low apron is formed by the inter-lateral plate without part of the anterior lateral plate being turned inwards, a feature which is seen apparently in a fairly early stage in *Kujdanowiaspis* (Stensiö, 1944: 27, text-fig. 17A). Then follows the condition seen in *Phlyctaenaspis* (Heintz, 1934a: 138, text-figs. 3–5), the inturned front quadrant of the anterior lateral being more clearly marked, and from this point Heintz (1931b: 237, text-fig. 10; 1938a: 24, text-fig. 7) derives a morphological series *Coccosteus*, *Dinichthys*, *Titanichthys*, *Heterostius*. It is clear that there were other types of development which involved the expansion of the anterior lateral part of the apron, as in the curious Downtonian form *Palaea-canthaspis* (Stensiö, 1944: 26, text-figs. 3, 4), the Upper and Middle Devonian ptyctodonts *Rhamphodontus* and *Rhamphodopsis* (Watson, 1934: 455, text-figs. 6, 7; 1938: 402, text-fig. 3); *Gemündina* (Watson, 1937: 138, text-fig. 25), and of course *Williamsaspis*.[1] All these formed the apron chiefly from the anterior lateral, especially *Williamsaspis*, in which the interlateral does not seem to have taken part at all, although the anterior dorsolateral did so substantially. The development of this peculiar feature to such a degree in such widely divergent forms is of no little interest, both from the systematic and the functional standpoint. What was the precise function of the apron is not clear. The obvious explanation is that it formed the hinder wall of the gill-chamber (Watson, 1938: 402) comparable to that formed by the shoulder-girdle in fishes generally, but there are differences. In the latter case the internal lamina is smooth and clearly marked off from the external part of the dermal shoulder-girdle; whereas in the arthrodires the apron is a direct modification of the dermal armour still bearing external ornamentation and doubtless covered by epidermis. In *Rhamphodopsis* the ornamentation appears to be similar to that of the external bones generally but lighter and fading out mesially, but in *Rhamphodontus* it is formed of peculiar, linearly arranged tubercles on the lower part only, while *Palaeacanthaspis* had a special triangular pyramidal ornamentation (Stensiö, 1944: 69, pl. vi, fig. 3; pl. ix, fig. 2; text-figs. 3, 7a), similar to that in *Williamsaspis* and differing only in that the tubercles are quite smooth and point backwards instead of forwards.[2] It is only in *Gemündina*, in Watson's (1937: text-fig. 25A) restoration, that

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[1] It would appear from Gross's sketch (1932: 27, text-fig. 11) that the apron was moderately well developed at least in *Hadrosteus* among the Wildungen brachythoracid arthrodires.

[2] The ornamentation on the interlateral in *Dinichthys* which, according to Heintz (1932: 176), is the

the apron is smooth and recessed in the manner to be expected of a true branchial wall.

It is difficult to see what use this ornament had, if the apron had formed the back of the gill-chamber and was covered in soft tissue, for it is very little raised above the surface of the bone, and indeed the fact that it faces different ways in different genera suggests that it was just ornament and had no other function. Moreover, it seems unlikely that such ornamentation would persist after the surface had become functionally an internal structure. One is tempted to suppose that in fact it was not internal and that the apron did not form the back wall of the gill-chamber, but that the flexible-throat or half-neck, which all arthrodires with movable heads must have had, in these forms with ornamented aprons, narrowed rapidly backwards and inwards from the jaws to the grooved mesial edge of the apron which is, as Heintz's series shows, the morphological front margin of the plates from which it was formed. It is quite clear that this was the case in such intermediate forms as *Phlyctaenaspis* and *Kujdanowiaspis* where the partly inturned front segment of the anterior lateral plate was still obviously part of the external surface and could not have functioned as the hinder wall of the gill-chamber (Text-fig. 39). The form of the mesial margin seems to support this idea, for the rising groove would appear to be due to the increase in thickness of the free integument.

In spite of a superficial resemblance, the arthrodire apron is quite different from the '*crista transversalis interna anterior*' of the antiarchs (Stensiö, 1931: 80, text-fig. 35; Gross, 1933*b*: 17, pl. 3, fig. 1, text-fig. 4A; Stensiö, 1948: 108, &c.) in both origin and function. The *crista* is an internal structure without ornament, formed by laminar processes from the inner surface of the bones, and bears the articular fossae; it is neither homologous nor analogous with the apron. Unless there was a connexion with breathing, as suggested above, the neck constriction and where developed, the apron, would seem to have more drawbacks than advantages. The area provided by the inner face of the apron would, of course, afford good anchorage for the body muscles, but the need for this is not obvious in a well-corseted form like *Williamsaspis*, although possibly more marked in those with contracted body-armour. On the other hand, the pocket between the back of the gill-chamber and the front of the apron seems a likely harbour for parasites, such as barnacles (Clarke, 1921: 62) and dirt, and during movement forwards with the head raised the pocket on each side would tend to impede progress, though not necessarily seriously in a slow-moving animal with well-developed pectoral fins. However, it seems to have had no markedly negative survival value. The occurrence of the apron among the arthrodires is peculiar, for the time spans almost the whole Devonian and the genera in which it is best developed are certainly not close relatives. As remarked before, all the arthrodires with a workable articulation between the head and body-armour must have had a soft neck to allow the upward movement of the head, and all may have had the constricted neck, but very few had a large apron, so that its development is not necessarily connected with that arthrodiran peculiarity. Nor does it seem connected with the habits in so far as one may deduce such matters from

only part of the armour in this genus to be ornamented, is seen in P.9395 to consist of fine tubercles with a triangular worn surface and the apex directed forwards.
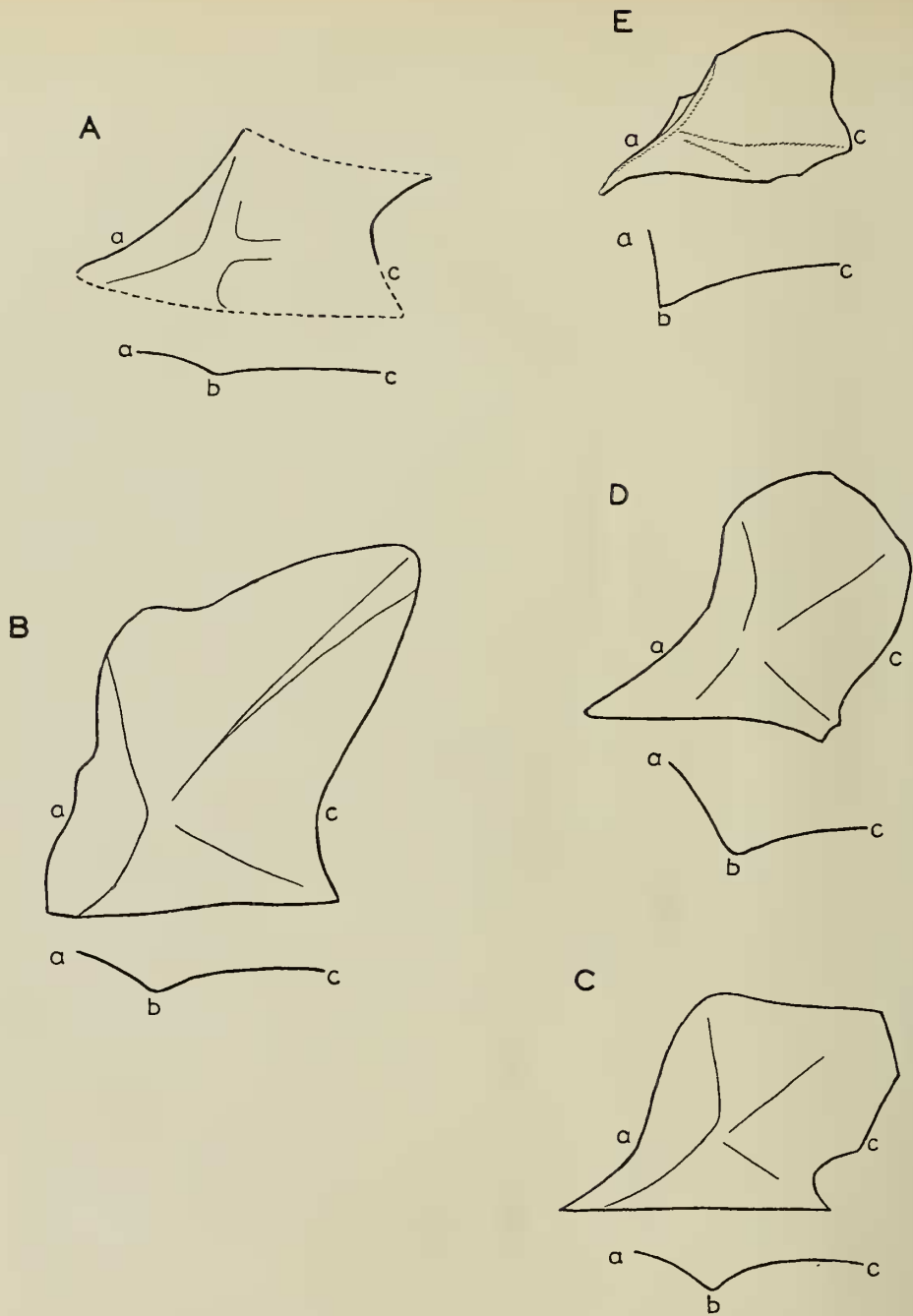
TEXT-FIG. 39. Sketches of left anterior lateral plates forming a morphological series to show development of the apron from the anterior quadrant of plate. A. *Arctolepis* [*Jaekelaspis*]. After Heintz, 1929. B. *Phlyctaenaspis*. After Heintz, 1934a. C. *Kujdanowiaspis*. After Stensiö, 1944. D. *Palaeacanthaspis*. After Stensiö, 1944. E. *Williamsaspis*. a–c, sections through growth-centre of plate, b. (All drawn so that length of section is constant.)

external form. The ptyctodonts had a wide, flat undersurface with large pectoral fin-spines in the same plane, and were presumably bottom-dwellers in fresh waters; *Williamsaspis* had a rounded undersurface (Text-fig. 12) with high pectoral keels and was probably an active marine swimmer, while *Palaeacanthaspis* with its flat bottom but smaller and somewhat raised pectoral fin-spines held an intermediate position. In fact the apron is the chief common factor between them, but we may note that all three seem to have been arctolepid derivatives. On the other hand, *Gemündina*, which stands apart by reason of its extreme specialization and the smooth recessed apron that may in fact have functioned as the wall of the branchial cavity, is for other reasons considered to be related to the brachythoracids.

VII. RELATIONSHIPS

During the last two decades very much information has come to hand concerning the arthrodires and their allies, mostly in the works of Heintz, Broili, Gross, and Watson, and from the numerous classical memoirs of Stensiö we have details of their internal structure far beyond our expectations. But as has often been pointed out, there is always the difficulty of separating characters due to relationship from those due to function, a difficulty that is particularly marked in extinct groups owing to the imperfect nature of our information and further confused by conflicting theories.

At the start we may accept Stensiö's (1944: 75; 1948: 222) view that the group 'Arthrodira' includes in it, as having a discernible common origin, not only the typical arthrodires, the Brachythoraci and the Arctolepida (Dolichothoraci), but all the oddly specialized groups variously associated with them—Acanthothoraci, Petalichthyida, Stegoselachii, Phyllolepida, Ptyctodontida, Rhenanida, and Antiarchi. All these may be expected to have a common ground-plan in internal structure which may or may not be masked in part externally by their particular specializations, yet still show in some simple functionally unimportant characters their proper relations one to another.[1]

The most obvious cleavage comes between the antiarchs and all the remainder. Westoll (1945b: 391) and Stensiö (1948: 147, 221–2, 613) both seem to derive this curious group directly from already armoured arthrodires, but this, as I have already suggested, I believe unlikely. The basic difficulty of the development of the antiarch arthropterygium seems under-estimated: Westoll postulates the development of articulations in the arctolepid spine: Stensiö (1944: 67) derives it from a fin such as he believes *Palaeacanthaspis* had and states that 'one may even suspect that the concentration had proceeded so far that the endoskeleton as a whole was of a mesorhachic ("archipterygial") type'. But apart from the unlikelihood of the development of articulations in a spine, Westoll's theory is based on a misunderstanding of the nature of the 'prespinal lamella'. Nor can I believe that the arthropterygium could be developed readily from a concentrated arthrodire fin as Stensiö (1948: 222) supposes, even were the mesorhachic nature of the acanthothoracid fin proved, which it is not—and no arthrodire is known with such a fin.

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[1] That 'the taxonomic significance of a character varies inversely as its functional value' is a principle of systematics which, if not always true, is always worth bearing in mind.

The general similarity between the armour of the antiarchs and that of the arcto-lepid arthrodires seems to me somewhat misleading, for the differences generally glossed over are important. Stensiö (1948: 189–211, 612) has made a profound comparison between the plates of the antiarchs and arthrodires, yet major difficulties remain unsolved even allowing for the distortions due to the specialization of the head and pectoral fins in the former group. Such 'soft' details as the sensory canals are fundamentally the same, as would be expected from common origin, but the patterns of the armour are no nearer to one another in detail than might be expected in independent development in related but already separated groups. The reversing of the ball-and-socket of the external articulations seems a clear indication of this independence, for the reversal in the antiarchs, were they developed from already armoured arthrodires, would be a complicated change without obvious benefit. As I see it the antiarchs developed from ancestral arthrodires before the development of the plate-armour.

Stensiö (1944) has shown the brachythoracids to be more primitive than the dolichothoracids in respect of their pectoral fins, but as mentioned above, they are more specialized in respect of their reduced body-armour. There can be little doubt that these two groups represent the two main branches of arthrodires from which all the other related groups, except the antiarchs, have been derived, and their common ancestor had the long-based fin of the brachythoracids and the long body-armour of the dolichothoracids. But the precise relationships of the other groups to them are not so easy to determine. These two groups are most obviously separated the one from the other on the length of the body-armour, but it is a character of functional importance and, although reduction in the brachythoracids is universal, it certainly could also have happened in the dolichothoracids—and did.

Stensiö (1944), in his important work on the acanthothoracids, has compared their specializations, particularly the short body-armour and the pectoral fin-bases, with the characters of all the other groups. He concludes (1944: 77) that although most nearly allied to the dolichothoracids they 'are to a certain extent intermediate in character between the Dolichothoraci (Acanthaspida) on the one hand and the Petalich-thyida, Stegoselachii, Phyllolepida, and Ptyctodontida on the other', and 'it has appeared that the differences between the Dolichothoraci (Acanthaspida) and the Brachythoraci are greater than what has been assumed hitherto'. Yet the neuro-cranium of Buchanosteus has shown yet one more fundamental similarity between the two main groups, while some of the resemblances noted between the acantho-thoracids and the others named seem to be due to functional convergence, parti-cularly in respect of the pectoral armour and fin. Nevertheless, all these groups must undoubtedly, as Stensiö says (1944: 77), 'be more closely allied to each other than has been believed by several previous writers' and some even more closely than Stensiö has suggested: for example, the acanthothoraceids are simply arctolepids specialized by the shortening, with the loss of some plates, of the body-armour and of the pectoral fin-base, and should be placed in a sub-group of the arctolepids.

The williamsosteids are also undoubtedly arctolepids and their pectoral fin-base and the unproduced spinal plate may show a more original type than the dolicho-thoracids with their enormous spines. In other words, Williamsaspis is possibly

a progenomorph,[1] that is, the little-modified survivor of the ancestral stock from which the more specialized forms, such as the dolichothoracids, were derived, although it may have suffered some reduction in the development of a spinal process.

The relationships of the other odd groups have not yet been clearly determined. Stensiö (1942: 23–25; 1944: 75; 1948: 222) places them all as equal orders in the Euarthrodira, although Westoll (1945b: 386, text-fig. 5) has attempted to link the rhenanids to the petalichthyids through the stegoselachian *Pseudopetalichthys*, as noted above. But a hint of affinities is given by one curious and otherwise possibly
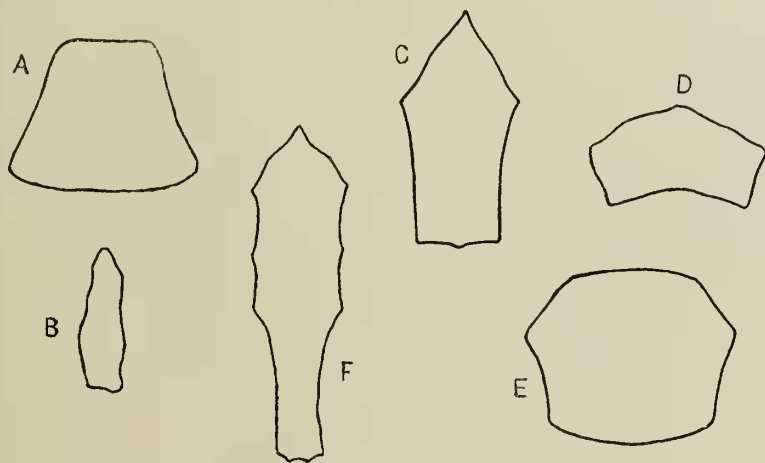
Text-fig. 40. Nuchal plates of the Euarthrodira, (*a*) a brachythoracid, (*b*) a rhenanid, (*c*) an arctolepid, (*d*) a ptyctodont, (*e*) a phyllolepid, (*f*) a petalichthyid. (After Heintz, Stensiö, Gross and Watson. Various scales.)

unimportant feature—the shape of the nuchal plate (Text-fig. 40). In all the brachythoracids this plate is widest behind, narrowing forwards, a feature shared only by the diminutive plate of the rhenanid *Asterosteus* (Stensiö, 1948: 194, text-fig. 69), and the rhenanids may be an early offshoot from early brachythoracids—at any rate they would come more readily from forms with a long fin-base than from petalichthyids.

All the other groups have the nuchal narrowing behind as in the dolichothoracids. This is most marked in petalichthyids which may have developed from arctolepid stock by the inwards and backwards migration of the orbits (Stensiö, 1948: 199, text-fig. 72). The phyllolepids (Stensiö, 1936: text-fig. 9) may have developed from the same group by the alteration in proportion of most plates, particularly by the lateral expansion of the nuchal plate and its fusion with the centrals, and the suppression of others in front. The ptyctodonts seem to have become specialized in the skull-roof by similar processes working in a different direction (Watson, 1938: text-fig. 2). All these groups, incidentally, carried well-developed pectoral spines.

[1] A typical progenomorph is the chordate *Jamoytius* (White, 1946) which has preserved the characters of the almost ideal vertebrate ancestor, lateral and median fin-folds, &c., until the Upper Silurian.

There remains only the Stegoselachii, a 'group' which is just a systematic dust-bin for arthrodires of uncertain position (Stensiö, 1942: 25). *Nessariostoma* and *Cratoselache*, the last of the arthrodires, are insufficiently known even for guessing their relationships, except for saying they have nothing to do with one another. *Pseudopetalichthys* and *Stensiöella* (Broili, 1933 *a*, *b*) seem to me possibly to be differently preserved versions of the same or a closely related animal in spite of the obvious discrepancies in the published interpretations of their structure, but without the opportunity of examining both specimens this is mere surmise. Broili's reference of both these forms to the petalichthyids may after all be not so far from the truth—they do not resemble any other group more than they do the petalichthyids, although the likeness there seems rather faint. On the published evidence I can see no reason for questioning Broili's (1933*b*: text-fig. 5) original interpretation of the shoulder-girdle of *Pseudopetalichthys* (see also Stensiö, 1944: text-fig. 18; Westoll, 1945*b*: text-fig. 5*c*), but if this is approximately correct, neither *Pseudopetalichthys* nor *Stensiöella* appears likely to have been derived from such forms as the contemporary *Lunaspis*, although they may represent the older less specialized stock.

Text-fig. 41 represents my present views on the relationships of the arthrodires to one another and may be expressed as follows:

Class ARTHRODIRA
    Division A. EUARTHRODIRA
        Order 1. Arctolepiformes
            Sub-order a. Arctolepidi
                Super-family i. Williamsostei
                Super-family ii. Dolichothoracei
                Super-family iii. Acanthothoracei
                          iv. (Ancestral ptyctodonts)
                          v. (Ancestral phyllolepids)
            Sub-order b. Ptyctodontidi
            Sub-order c. Phyllolepidi
            Sub-order d. Petalichthyidi
            Sub-order e. Stensiöellidi
        Order 2. Coccosteiformes
            Sub-order a. Brachythoracidi
            Sub-order b. Rhenanidi
    Division B. ANTIARCHA

This classification differs considerably from most of those recently published (Gross, 1937: 50; Watson, 1937: 143; Moy-Thomas, 1939: 124; Berg, 1940: 365; Romer, 1945: 574–5; Westoll, 1945*b*: 394), except that of Stensiö (1944: 75; 1948: 222), who first demonstrated the relationships between the various sub-orders grouped above in the order Arctolepiformes. It does, however, differ somewhat in emphasis from Stensiö's arrangement and is based on different argument.

Such a classification may be criticized for the reason that the stratigraphical background has been ignored in that the known times of the first appearance of the various

groups are not in keeping with the supposed derivations, and this is to some extent true. But there are no certain connecting links between any of the groups, all of which are by the known records discrete; our knowledge is hopelessly inadequate in any case, and the length of the supposed missing chain is not a matter to outweigh arguments based on known form.
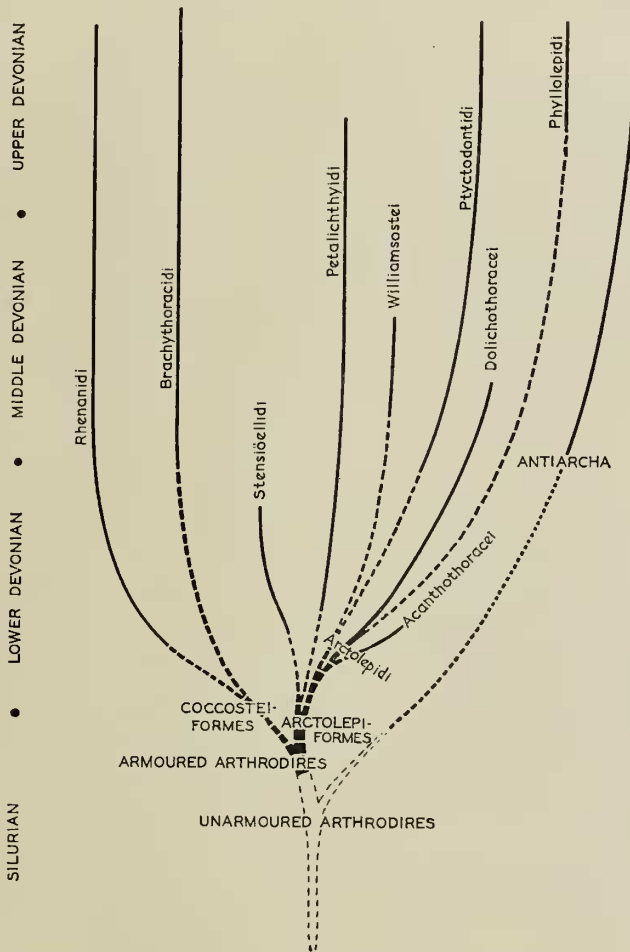
TEXT-FIG. 41. Suggested relationships of the arthrodires.

There remains to me only the pleasant duty of expressing my thanks to those from whom I have received assistance. Firstly my thanks are due to Mr. W. E. Williams, the discoverer of the fossils, who gave them to the British Museum (Natural History), and then to Mr. R. Bedford for the active part he played in bringing them to my notice, while Mr. C. St. J. Mulholland, Government Geologist of New South Wales, kindly allowed me to examine the unique specimen of *Notopetalichthys*. Mr. H. A. Toombs,

as always, has been my right hand, and to him much praise is due for his skill in developing the specimens.

To my friends, Professor Erik Stensiö and Professor Stanley Westoll I am indebted for helpful and stimulating discussions, even though our conclusions have not always coincided.

Finally, I have to thank Mr. R. Baker and Mr. F. M. Wonnacott for assistance in the preparation of the manuscript.

Since this paper was written I have again had the very great pleasure of visiting the Paleozoological Department of the Swedish Museum of Natural History, Stockholm, where Professor E. A. Stensiö most generously placed at my disposal the whole of his superb preparations of arthrodire material and the typescripts of four monumental works relating to them, in which the shoulder-girdles of at least a dozen Wildungen genera are described. It is difficult adequately to express my indebtedness to Professor Stensiö for his generosity and kindness.

Later I travelled to Oslo, where I enjoyed the hospitality of Professor Anatol Heintz at home and in the Paleontological Museum, and availed myself of my friend's wide knowledge of the group. My warmest thanks are due to both Professor and Mrs. Heintz for their kindness.

VIII. REFERENCES

AGASSIZ, L. 1844–1845. *Monographie des Poissons Fossiles du Vieux Grès Rouge.* xxxvi+ 171 pp., 42 pls. (col.). Neuchâtel & Soleure.

BERG, L. S. 1940. Classification of Fishes, both Recent and Fossil. *Trav. Inst. zool. Acad. Sci. URSS*, **5**, 2 : 517 pp., 190 figs.

BROILI, F. 1933*a*. Weitere Fischreste aus den Hunrückschiefern. *S. B. bayer. Akad. Wiss.*, **1933**: 269–313, 6 pls., 15 text-figs.

—— 1933*b*. Ein Macropetalichthyide aus den Hunsrückschiefern. *S. B. bayer. Akad. Wiss.*, **1933**: 417–437, 1 pl., 7 text-figs.

BRYANT, W. L. 1934. The Fish fauna of Beartooth Butte, Wyoming. Parts II and III. *Proc. Amer. Phil. Soc.*, **73**: 127–162, 26 pls., 8 text-figs.

CHAPMAN, F. 1916. On the generic position of '*Asterolepis ornata* var. *australis*' McCoy. *Proc. Roy. Soc. Vict.*, Melbourne (n.s.), **28**: 211–215, 2 pls.

CLARKE, J. M. 1921. Organic dependence and disease. *Bull. N.Y. St. Mus.*, Albany, **221–222**: 113 pp., 105 text-figs.

DENISON, R. H. 1950. A new Arthrodire from the New York State Devonian. *Amer. J. Sci.*, **248**: 565–580, 3 pls., 5 text-figs.

—— 1951. Evolution and classification of the Osteostraci. *Fieldiana*, Chicago (Geol.), **11**: 157–196, 12 text-figs.

DUNKLE, D. H. 1947. A new genus and species of Arthrodiran Fish, &c. *Sci. Pub. Cleveland Mus. Nat. Hist.* **8**, 10: 103–117, 5 text-figs.

DUNKLE, D. H., & BUNGART, P. A. 1946. The Antero-supragnathal of *Gorgonichthys. Amer. Mus. Nov.* **1316**: 10 pp., 4 text-figs.

EGERTON, P. G. 1860. Palichthyologic Notes, No. 12. Remarks on the nomenclature of the Devonian Fishes. *Quart. J. Geol. Soc. Lond.* **16**: 119–136, 9 text-figs.

GEUENICH, E. 1939. Paläobiologische Studien an Arthrodiren. *Palaeobiologica*, **7**: 10–29, 4 figs.

GRAY, J. 1933. Directional control of Fish movement. *Proc. Roy. Soc. Lond.* (B), **113**: 115–125, 5 pls., 3 text-figs.

GROSS, W.   1930.   Die Fische des mittleren Old Red Süd-Livlands. *Geol. paläont. Abh.*, (n.F.), **18:** 123–156, 5 pls.

—— 1932.   Die Arthrodira Wildungens. *Geol. paläont. Abh.*, (n.F.), **19:** 1–61, 2 pls., 26 text-figs.

—— 1933*a*.   Die unterdevonischen Fische . . . von Overath. *Abh. preuss. geol. Landesanst.*, (n.F.), **145:** 41–77, 7 pls., 16 text-figs.

—— 1933*b*.   Die Wirbeltiere des rheinischen Devons. *Abh. preuss. geol. Landesanst.*, (n.F.), **154:** 83 pp., 11 pls., 20 text-figs.

—— 1933*c*.   Die Fische des baltischen Devons. *Palaeontographica*, Stuttgart, **79A:** 1–74, 6 pls.

—— 1935.   Histologische Studien am Aussenskelett fossiler Agnathen und Fische. *Palaeontographica*, Stuttgart, **83A:** 1–60, 14 pls.

—— 1937.   Die Wirbeltiere des rheinischen Devons II. *Abh. preuss. geol. Landesanst.*, (n.F.), **176:** 1–83, 29 text-figs.

—— 1938*a*.   *Rhachiosteus pterygiatus* n.gen. n.sp. (Euarthrodira, Brachythoraci). *Decheniana*, Bonn, **97A:** 183–208, 4 pls., 6 text-figs.

—— 1938*b*.   Über das Spinale und die angrenzenden Knochen der Brachythoraci. *N. Jb. Min. Geol. Paläont.*, Beil.-Bd. **79B:** 403–418, 3 pls., 3 text-figs.

—— 1940.   Acanthodier und Placodermen aus *Heterostius*-Schichten Estlands und Lettlands. *Ann. Soc. Reb. Nat. Invest. Univ. Tartu*, **46:** 1–88, 9 pls., 17 text-figs.

GROVE, A. J., & NEWELL, G. E.   1936.   A mechanical investigation into the effectual action of the caudal fin of some aquatic chordates. *Ann. Mag. Nat. Hist.*, (10), **17:** 280–290, 4 text-figs.

HARRIS, J. E.   1936.   The role of the fins in the equilibrium of the swimming Fish, I. *J. Exp. Biol.*, Cambridge, **13:** 476–493, 8 text-figs.

HEINTZ, A.   1929.   Die downtonischen und devonischen Vertebraten von Spitzbergen, II. Acanthaspida. *Skr. Svalb. og Ishavet*, **22:** 1–81, 24 pls., 37 text-figs.

—— 1931*a*.   Revision of the structure of *Coccosteus decipiens* Ag. *Norsk geol. Tidsskr.*, **12:** 291–313, 2 pls., 12 text-figs.

—— 1931*b*.   Untersuchungen über den Bau der Arthrodira. *Acta zool.*, Stockh., **12:** 225–239, 2 pls., 11 text-figs.

—— 1931*c*.   A reconstruction of *Stenognathus gouldi* (Newberry). *Ann. Mag. Nat. Hist.*, (10), **8:** 242–249, 5 text-figs.

—— 1932.   The structure of *Dinichthys*, &c. *Amer. Mus. Nat. Hist., Bashford Dean Mem. Vol.* **4:** 115–224, 9 pls.

—— 1934*a*.   Some remarks about the structure of *Phlyctaenaspis acadica* Whiteaves. *Norsk. geol. Tidsskr.*, **14:** 127–144, 3 pls., 6 text-figs.

—— 1934*b*.   Revision of the Estonian Arthrodira. Pt. 1. Family Homostiidae Jaekel. *Arch. naturk. Estlands* (1), **10**, 4: 177–290, 13 pls., 51 text-figs.

—— 1935.   How the Fishes learned to swim. *Ann. Rep. Smithson. Instn.*, **1934:** 223–245, 12 text-figs.

—— 1937.   Die downtonischen und devonischen Vertebraten von Spitzbergen, VI. Lunaspis-Arten aus dem Devon Spitzbergens. *Skr. Svalb. og Ishavet*, **72:** 1–23, 1 pl., 4 text-figs.

—— 1938*a*.   Notes on Arthrodira. *Norsk geol. Tidsskr.*, **18:** 1–27, 3 pls., 7 text-figs.

—— 1938*b*.   Über die ältesten bekannten Wirbeltiere. *Naturwissenschaften*, **26:** 49–58, 4 text-figs.

HILLS, E. S.   1936.   On certain endocranial structures in *Coccosteus*. *Geol. Mag.*, Lond. **73:** 213–226, 1 pl., 6 text-figs.

—— 1941.   The cranial roof of *Dipnorhynchus sussmilchi* (Eth. fil.). *Rec. Aust. Mus.*, **21:** 45–55, 1 pl., 6 text-figs.

HOLMGREN, N.   1942.   Studies on the head of fishes. Part III. The phylogeny of Elasmobranch Fishes. *Acta zool.*, Stock., **23:** 129–261, 54 text-figs.

JAEKEL, O.   1907.   Über *Pholidosteus* nov. gen., die Mundbildung und die Körperform der Placodermen. *S. B. Ges. naturf. Fr. Berl.*, **1907:** 170–186, 6 text-figs.

KERMACK, K. A.   1943.   The functional significance of the hypocercal tail in *Pteraspis rostrata*. *J. Exp. Biol.*, Cambridge, **20:** 23–27, 5 text-figs.

McCoy, F. 1876. *Prodromus of the Palaeontology of Victoria*, **4:** 19–20, 1 pl. Geol. Surv., Victoria.

Moy-Thomas, J. A. 1939. *Palaeozoic Fishes.* ix+149 pp., 32 text-figs. London.

Ribbing, L. 1938. Die Muskeln und Nerven der Extremitäten. *In* Bolk, L. *Handbuch der vergleichenden Anatomie der Wirbeltiere*, **5:** 543–656, 85 text-figs.

Romer, A. S. 1945. *Vertebrate Paleontology.* 2nd ed. ix+687 pp., 377 figs. Chicago.

Stensiö, E. A. 1925. On the head of the Macropetalichthyids. *Field Mus. Publ.*, **232** (Geol. 4): 85–198, 31 pls., 26 text-figs.

—— 1931. Upper Devonian Vertebrates from East Greenland. *Medd. Grønland*, **86,** 1: 212 pp., 36 pls., 95 text-figs.

—— 1934a. On the heads of certain Arthrodires, I. *K. svenska VetenskAkad. Handl.*, (3) **13,** 5: 1–79, 14 pls., 30 text-figs.

—— 1934b. On the Placodermi of the Upper Devonian of East Greenland, I. Phyllolepida and Arthrodira. *Medd. Grønland*, **97:** 1–58, 25 pls., 25 text-figs.

—— 1936. On the Placodermi of the Upper Devonian of East Greenland. Supplement to Part I. *Medd. Grønland*, **97,** 2: 52 pp., 30 pls., 26 text-figs.

—— 1942. On the snout of Arthrodires. *K. svenska VetenskAkad. Handl.*, (3) **20,** 3: 1–32, 14 text-figs.

—— 1944. Contributions to the knowledge of the vertebrate fauna of the Silurian and Devonian of Western Podolia, II. Notes on two Arthrodires from the Downtonian of Podolia. *Ark. Zool.*, Uppsala, **35A,** 9: 1–83, 14 pls., 19 text-figs.

—— 1945. On the heads of certain Arthrodires, II. *K. svenska VetenskAkad. Handl.*, (3) **22:** 1–70, 14 text-figs.

—— 1948. On the Placodermi of the Upper Devonian of East Greenland, II. Antiarchi: Subfamily Bothriolepinae. *Palaeozool. Grønland*, **2:** 622 pp., 75 pls., 308 text-figs.

—— 1950. La Cavité labyrinthique, l'Ossification sclérotique et l'Orbite de *Jagorina*. *In* George, A. *Paléontologie et Transformisme*, pp. 9–41, 8 text-figs. Paris.

Stensiö, E. A., & Jarvik, E. 1939. Agnathi und Pisces. *Fortschr. Paläont.*, Berlin, **2:** 254–295.

Toombs, H. A. 1948. The use of acetic acid in the development of vertebrate fossils. *Mus. Journ., Lond.* **48:** 54–55, 1 pl.

Watson, D. M. S. 1934. The interpretation of the Arthrodires. *Proc. Zool. Soc. Lond.*, **1934:** 437–464, 1 pl., 8 text-figs.

—— 1935. Fossil Fishes of the Orcadian Old Red Sandstone. *In* Geology of the Orkneys. *Mem. Geol. Surv. Scotland*, pp. 157–169, 15 text-figs.

—— 1937. The Acanthodian Fishes. *Philos. Trans.* (B), **228:** 49–146, 10 pls., 25 text-figs.

—— 1938. On *Rhamphodopsis*, a Ptyctodont from the Middle Old Red Sandstone. *Trans. Roy. Soc. Edinb.* **59:** 397–410, 1 pl., 5 text-figs.

—— 1950. Discussion on Stensiö, 1950. *In* George, A. *Paléontologie et Transformisme*, pp. 41–43. Paris.

Westoll, T. S. 1945a. A new Cephalaspid Fish from the Downtonian of Scotland, &c. *Trans. Roy. Soc. Edinb.* **61:** 341–357, 1 pl., 7 text-figs.

—— 1945b. The paired fins of Placoderms. *Trans. Roy. Soc. Edinb.* **61:** 381–398, 9 text-figs.

White, E. I. 1935. The Ostracoderm *Pteraspis* Kner and the relationships of the Agnathous vertebrates. *Philos. Trans.* (B), **225:** 381–457, 3 pls., 97 text-figs.

—— 1946. *Jamoytius kerwoodi*, a new Chordate from the Silurian of Lanarkshire. *Geol. Mag., Lond.* **83:** 89–97, 2 text-figs.

Woodward, A. S. 1891. *Catalogue of the Fossil Fishes*, **2:** 567 pp., 16 pls., 58 text-figs. Brit. Mus. (Nat. Hist.), London.

—— 1941. The head shield of a new Macropetalichthyid fish (*Notopetalichthys hillsi*, gen. et sp. nov.) from the Middle Devonian of Australia. *Ann. Mag. Nat. Hist.* (11), **8:** 91–96, 1 pl., 1 text-fig.

LETTERING USED IN TEXT-FIGURES

AbA	Attachment area of abductor muscles.
AbM	,, ,, ,,
AbP	,, ,, ,,
AdA	Attachment area of adductor muscles.
ADL	Anterior dorsolateral plate.
AdM	Attachment area of adductor muscles.
AdP	,, ,, ,,
AL	Anterior lateral plate.
AL″	Internal impression of anterior lateral plate.
ALA	Apron of anterior lateral plate.
ALA(L)	Apron of left anterior lateral plate.
AMA	Anterior mesial angle of coracoid.
AMV	Anterior median ventral plate.
APo	Anterior postorbital process.
AR	Articular facet for anterior ? fin-ray.
Ar	Broken base of articular surface.
AVL	Anterior ventrolateral plate.
BE	Undersurface of neurocranium.
BO	Branchial opening.
CE	Central plate.
COA	Area of overlap on to central plate.
csg	Central sensory groove.
Cv	Cavum cerebrale cranii.
C+N	Centronuchal plate.
DE	External opening of ductus endolymphaticus.
Fl	Mesial flange.
FSO	Fin socket.
Gl–Gl	Articular area for radials.
Gr	Groove on mesial edge of apron.
IL	Interlateral plate.
ILi	Inner perichondrial bone of interlateral plate.
IL(L)	Left interlateral plate.
ioc	Infraorbital groove.
JV	Vein draining into jugular vein from ventral surface.
lc	Main lateral line groove.
MA	Marginal plate.
MC	Median cusp.
MD	Median dorsal plate.
MOA	Area of overlap on to marginal plate.
mp	Median pit-line groove.
MSP	Mesial process of posterior superognathal.
N	Branches of 10th nerve.
N′	Exit of branches of 10th nerve.
NOA	Area overlapped by nuchal plate.
NU	Nuchal plate.
OLA	Overlapping area of anterior lateral plate on anterior dorso-lateral plate.
OLP	Overlapping area of posterior lateral plate on posterior dorso-lateral plate.
OM	Orbital margin.
Or	Inner wall of orbit.

ORB	Orbit.
PAN	Paranuchal plate.
PDL	Posterior dorsolateral plate.
PF	Pectoral fin.
Pi	Pineal plate.
PL	Posterior lateral plate.
PM	Postmarginal plate.
PmOA	Area of overlap on to postmarginal plate.
PMV	Posterior median ventral plate.
poc	Preopercular groove.
pp	Posterior pit-line groove.
PPo	Posterior postorbital process.
PRO	Preorbital plate.
PTO	Postorbital plate.
PVL	Posterior ventrolateral plate.
R	Rostral plate.
Sc. 1–5	Scars.
Sc Co	Scapulo-coracoid cartilage.
SHy	Hyoid vein.
SO	Pectoral fenestra.
soc	Suborbital groove.
SP	Spinal plate.
SS	Suborbital shelf.
SV	Supravagal process.
VC	Vascular canals.
VJu	Jugular vein.
VJu′	Exit of jugular vein.

PLATE 26

Williamsaspis bedfordi gen. et sp. nov.

Fig. 1. Ventral view of carapace. The holotype, P.27073, × 1½. (For explanation see Text-fig. 3.)

Fig. 2. Left side view of same, lit from below. × 1½. (For explanation see Text-fig. 7.)